University of Alberta

The taxonomy and biology of myxotrichaceous fungi from a Sphagnum *bog in Alberta, Canada*

by

Adrianne Vanessa Rice ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the

requirements for the degree of *Doctor of Philosophy*

in

Environmental Biology and Ecology

Department of *Biological Sciences*

Edmonton, Alberta

Fall 2005

Library and
Archives Canada

Published Heritage
Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et
Archives Canada

Direction du
Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

0-494-08721-8

Your file *Votre référence*
ISBN:
Our file *Notre reterence*
ISBN:

NOTICE:
The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distribute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

AVIS:
L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

For my family who have always believed in and supported me in all of my decisions and to my friends who are family away from home.

ABSTRACT

Bogs store vast amounts of carbon (C) due to slow decomposition of *Sphagnum*. Global warming could increase decomposition and C mobilization. Lignin- and cellulose-degrading fungi are primary decomposers of *Sphagnum* but their diversity and temperature responses are poorly known. Psychrotolerant species of *Myxotrichaceae* (*Ascomycota*) were abundant from peat and wood bait. *Oidiodendron maius* was the most common species on moist incubated peat while *Geomyces pannorum* was most abundant on peat cultured on Mycosel® agar and on bait in moist chambers and on Mycosel® agar. Six *Oidiodendron* species and two *Pseudogymnoascus* species were isolated from bait. Their abundance suggests they may be important decomposers of peat.

Accurate ecological assessment of these species required taxonomic clarification. Morphology and physiology, including Biolog® FF profiles, distinguished 25 *Oidiodendron* species, including *O. fimicolum*, a new species from mushroom compost, and two unnamed species from Perryvale Bog. *Oidiodendron fuscum* was reinstated as the generic type, *O. citrinum* was transferred to *O. maius* as *O. maius* var. *citrinum*, and *O. scytaloides, O. reticulatum*, and *O. ramosum* were shown to be synonyms of *O. chlamydosporicum, O. hughesii*, and *O. setiferum* respectively, and *O. robustum* and *O. terrestre* were excluded. *Pseudogymnoascus appendiculatus* and *P. verrucosus* were described from Perryvale Bog and a key was provided to four taxa in *Pseudogymnoascus*. The new species had characters intermediate between *Pseudogymnoascus* and *Gymnostellatospora*, prompting a re-evaluation of these genera and anamorphs in *Geomyces*. ITS sequence data support the distinction between *Gymnostellatospora* and *Pseudogymnoascus* but indicate that *Geomyces* is polyphyletic.

In vitro assessments suggest *Myxotrichaceae* can decompose *Sphagnum* at current temperatures. Most species degraded cellulose and soluble phenolics and caused 0-50% mass loss of *Sphagnum*. In contrast, two basidiomycetes degraded cellulose and insoluble phenolics and caused 0-35% mass loss. The *Myxotrichaceae* eroded the *Sphagnum* leaf cell walls in a

pattern resembling simultaneous white rot of wood, while the decay caused by the basidiomycetes resembled preferential white rot. These results indicate *Myxotrichaceae* can release C and nutrients from peat, playing an important role in nutrient cycling. Their importance may be increased by their formation of mycorrhizal associations with dominant peatland plants.

ACKNOWLEDGEMENTS

First, I gratefully acknowledge my supervisor, Dr. Randy Currah, whose enthusiasm for mycology and research was instrumental in my decision to pursue graduate research. Randy, I could never have completed this project without your continuous and enthusiastic support. Drs. Lynne Sigler and Julia Foght provided advice, guidance, and different perspectives on my project as members of my supervisory committee. Thanks to Lynne for help with taxonomic matters, accessioning cultures, and reading and commenting on drafts of my manuscripts. Thanks to Julia for reminding me of the bigger picture and encouraging me to think about bacteria as well as fungi. Special thanks to my examininers: Drs. Stephen Strelkov and Gary Samuels for taking time out of their busy schedules to read my thesis and provide constructive comments.

This research would have been impossible without the assistance of other scientists. Dr. Aki Tsuneda and George Braybrook assisted with Scanning Electron Microscopy. Dr. Connie Gibas assisted with molecular work and made working with DNA a pleasure. Dr. Sarah Hambleton shared unpublished images and phylogenetic trees and examined the type of *Periconia tenuissima*. Field and laboratory assistance were provided by Lindsay Elliott, Melissa Day, Ben Wilson, and Marcie Plishka. I also acknowledge the support and friendship of my fellow grad students in the Currah lab over the past six years: Markus Thormann, Melissa Piercey, Grace Hill-Rackette, Connie Gibas, Matt Greif, Mike Schulz, Winnie Wang, Sam Skinner, Melissa Day, and Marie Davy, and other visitors to the lab.

I thank my partner Brad Lindseth, who was coerced into acting as unpaid driver, field assistant, and lab slave, as well as providing moral support and encouragement. My mom, Ann Rice, also accompanied me into the field and provided encouragement and support.

Funding was provided by Natural Sciences and Engineering Research Council of Canada (NSERC) Research Grants to R.S. Currah and NSERC PGS-A and PGS-B Scholarships, a University of Alberta Dissertation Fellowship, a Canadian Circumpolar Institute C/BAR research grant, and an Alberta Conservation Association Biodiversity Grant to the author.

TABLE OF CONTENTS

Chapter **Page**

1. An overview of the *Myxotrichaceae*, peatlands, and the history of *Myxotrichaceae* in peat....1
    - 1.1. The *Myxotrichaceae* (*Ascomycota*)....2
        - 1.1.1. Genera in the *Myxotrichaceae*....2
            - 1.1.1.1. *Myxotrichum*....3
            - 1.1.1.2. *Pseudogymnoascus*....3
            - 1.1.1.3. *Gymnostellatospora*....4
            - 1.1.1.4. *Geomyces*....4
            - 1.1.1.5. *Oidiodendron*....5
        - 1.1.2. Taxonomic History....5
        - 1.1.3. Distribution, Occurrence, and Ecology....6
    - 1.2. Peatlands....8
        - 1.2.1. Bogs....9
        - 1.2.2. Decomposition of *Sphagnum*....9
    - 1.3. Fungi from peatlands....10
    - 1.4. *Myxotrichaceae* from peat....12
    - 1.5. Taxonomic relationships among myxotrichaceous fungi....12
    - 1.6. Potential ecological roles of myxotrichaceous fungi in peat....13
    - 1.7. Literature Cited....13

2. New perspectives on the niche and holomorph of the myxotrichoid hyphomycete, *Oidiodendron maius*....22
    - 2.1. Introduction....22
    - 2.2. Materials and Methods....23
        - 2.2.1. Fungal isolation....23
        - 2.2.2. Crossing trials....23
    - 2.3. Results and Discussion....24
        - 2.3.1. Assessment of *Oidiodendron maius* in bog peat....24
        - 2.3.2. Sterile myxotrichoid ascomata produced by *Oidiodendron maius*....25
    - 2.4. Literature Cited....32

3. Profiles from Biolog FF plates and morphological characteristics support the recognition of *Oidiodendron fimicolum* sp. nov……34
    3.1. Introduction……34
    3.2. Materials and Methods……35
    3.3. Results……36
        3.3.1. Biolog……36
        3.3.2. Taxonomy……38
    3.4. Discussion……39
    3.5. Literature Cited……48

4. *Oidiodendron*: A survey of the named species and related anamorphs of *Myxotrichum*……49
    4.1. Introduction……49
        4.1.1. Taxonomic History……50
        4.1.2. Distribution, Occurrence, and Ecology……53
    4.2. Materials and Methods……56
        4.2.1. Morphology……56
        4.2.2. Physiological Studies……57
    4.3. Evaluation of key characters……58
        4.3.1. Morphology……58
        4.3.2. Physiology……61
    4.4. Keys to *Oidiodendron* species……62
        4.4.1. Synoptic key to *Oidiodendron* species……62
        4.4.2. Dichotomous key to *Oidiodendron* species……67
    4.5. Species descriptions……70
        1. *Oidiodendron* anamorph of *Myxotrichum arcticum*……70
        2. *Oidiodendron* anamorph of *Myxotrichum cancellatum*……71
        3. *Oidiodendron* anamorph of *Myxotrichum emodense*……71
        4. *Oidiodendron* anamorph of *Myxotrichum setosum*……72
        5. *Oidiodendron* anamorph of *Myxotrichum striatosporum*……73
        6. *Oidiodendron ambiguum*……74
        7. *Oidiodendron cerealis*……74
        8. *Oidiodendron chlamydosporicum*……75
        9. *Oidiodendron echinulatum*……76
        10. *Oidiodendron fimicolum*……77

11. *Oidiodendron flavum*....................77
12. *Oidiodendron fuscum*....................78
13. *Oidiodendron griseum*....................79
14. *Oidiodendron hughesii*....................81
15. *Oidiodendron maius* var. *citrinum*....................82
16. *Oidiodendron maius* var. *maius*....................83
17. *Oidiodendron muniellense*....................84
18. *Oidiodendron myxotrichoides*....................85
19. *Oidiodendron periconioides*....................86
20. *Oidiodendron pilicola*....................87
21. *Oidiodendron rhodogenum*....................87
22. *Oidiodendron setiferum*....................88
23. *Oidiodendron tenuissimum*....................89
24. *Oidiodendron truncatum*....................90
4.6. Excluded species....................90
4.7. Literature cited....................143

5. Two new species of *Pseudogymnoascus* with *Geomyces* anamorphs and their phylogenetic relationship with *Gymnostellatospora*....................149
5.1. Introduction....................149
5.2. Materials and Methods....................150
5.2.1. Isolation and description of the new species....................150
5.2.2. DNA sequencing....................151
5.3. Results....................152
5.3.1. Taxonomy....................152
5.3.2. DNA Sequencing....................155
5.4. Discussion....................156
5.5. Literature Cited....................171

6. *In vitro* decomposition of *Sphagnum* by microfungi resembles white rot of wood....................174
6.1. Introduction....................174
6.2. Methods....................175
6.2.1. Isolation of fungi....................175
6.2.2. Enzyme assays....................176

6.2.3. Mass loss studies....177
6.2.4. SEM observations....177
6.3. Results....178
6.4. Discussion....179
6.5. Literature Cited....193

7. *Oidiodendron maius*: Saprobe in *Sphagnum* peat, mutualist in ericaceous roots?....198
7.1. Introduction....198
7.2. *Oidiodendron maius*....200
7.3. *Oidiodendron maius* as saprobe....201
7.4. Ericoid mycorrhizas....204
7.5. *Oidiodendron maius* as an ericoid mycorrhizal fungus....206
7.6. Significance and relevance....208
7.7. Conclusions....210
7.8. Literature cited....218

8. Conclusions....227
8.1. *Myxotrichaceae* in peatlands....227
8.2. Taxonomic considerations....228
8.3. Potential ecological roles....230
8.4. Future directions....232
8.5. Literature Cited....234

Appendix 1. Biolog® FF substrates....240

Appendix 2. Biolog FF profiles of 43 *Oidiodendron* and *Myxotrichum* isolates....242

Appendix 3. Accession information for *Myxotrichaceae* deposited at the University of Alberta Microfungus Collection and Herbarium (UAMH)....258

Appendix 4. Glossary of terms....259

LIST OF TABLES

Table **Page**

2.1. Location and collection sites for 21 isolates of *Oidiodendron maius* used in a series of controlled crosses established on sterilized thalli of *Cladonia* spp……………..................27

2.2. Observational frequencies (as % of plates with sporulating colonies) of *Oidiodendron maius* compared with *Geomyces, Penicillium* and *Mucor* (the three most common genera isolated from bog peat)……………………………………………………………………28

2.3. Crosses among 18 isolates of *Oidiodendron maius* that produced sterile gymnothecia on sterilized *Cladonia* after 6 mo incubation…………………….......................................29

3.1. Isolate, species, collector, and collection information for isolates of *Oidiodendron* and *Myxotrichum* species used in the Biolog FF assessment……………………………………42

4.1. Sources and enzymatic profiles for *Oidiodendron* isolates studied…………………………92

4.2. Conidial shapes in *Oidiodendron* species……………………………………………………..94

5.1. Species, strain, and collection information for newly sequenced species of *Pseudogymnoascus*, *Gymnostellatospora*, and *Geomyces*…………………….................160

6.1. Observational frequencies of the four most frequently recovered genera from lignin-rich bait blocks placed in Perryvale Bog……………………………………………………………186

6.2. Enzyme assay results and percentage mass losses of *Sphagnum* for six *Oidiodendron* species, *Geomyces pannorum*, two *Pseudogymnoascus* species, *Bjerkandera adusta*, and *Phanerochaete chrysosporium*……………………………………………………………187

LIST OF FIGURES

Figure **Page**

2.1. Sterile gymnothecia produced by *Oidiodendron maius* (UAMH 9749 crossed with UAMH 10460) after four months incubation on sterilized *Cladonia* and gymnothecia of *Myxotrichum arcticum* (UAMH 7565)……………………………………………………31

3.1. Representative dendrogram of 54 Biolog FF plate data sets for 42 isolates, representing 19 *Oidiodendron* and *Myxotrichum* species ……………………………………………45

3.2. Conidiophores and conidia of *O. fimicolum* Rice & Currah, sp. nov.……………………47

4.1. *Oidiodendron* anamorph of *Myxotrichum arcticum*……………………………………96

4.2. *Oidiodendron* anamorph of *Myxotrichum cancellatum* (UAMH 1996)……………………98

4.3. *Oidiodendron* anamorph of *Myxotrichum emodense*. Reproduced with permission from Udagawa & Uchiyama 1999 (Figures 13, 14)……………………………………………100

4.4. *Oidiodendron* anamorh of *Myxotrichum setosum* (UAMH 3835)……………………102

4.5. *Oidiodendron* anamorph of *Myxotrichum striatosporum* (UAMH 3758)………………104

4.6. *Oidiodendron ambiguum*. Reconstructed from Peyronel (1914) and Malan (1949)……106

4.7. *Oidiodendron cerealis* (UAMH 1522)……………………………………………………108

4.8. *Oidiodendron chlamydosporicum*……………………………………………………110

4.9. *Oidiodendron echinulatum* (UAMH 8467)…………………………………………………112

4.10. *Oidiodendron fimicolum* (UAMH 10459)…………………………………………………114

4.11. *Oidiodendron flavum* (UAMH 1524)……………………………………………………116

4.12. *Oidiodendron fuscum* (UAMH 8511)....................118

4.13. *Oidiodendron griseum*....................120

4.14. *Oidiodendron hughesii*. Reproduced with permission from Udagawa & Uchiyama 1998 (Figures 11, 14, 17) and Calduch *et al.* 2004 (Figures 24, 27, 31)....................122

4.15. *Oidiodendron maius* var. *citrinum* (UAMH 1525)....................124

4.16. *Oidiodendron maius* var. *maius*....................126

4.17. *Oidiodendron muniellense*. Reproduced with permission from Calduch *et al.* 2004 (Figures 2, 3, 6)....................128

4.18. *Oidiodendron myxotrichoides*. Reproduced with permission from Calduch *et al.* 2002 (Figures 1, 10)....................130

4.19. *Oidiodendron periconioides* (UAMH 8527)....................132

4.20. *Oidiodendron pilicola*. Reconstructed from Kobayasi (1969)....................134

4.21. *Oidiodendron rhodogenum* (UAMH 1405)....................136

4.22. *Oidiodendron setiferum* (UAMH 5715) or reproduced with permission from Calduch *et al.* 2004 (Figures 12, 18)....................138

4.23. *Oidiodendron tenuissimum*....................140

4.24. *Oidiodendron truncatum*....................142

5.1. Light micrographs of *Pseudogymnoascus appendiculatus*....................162

5.2. Scanning electron micrographs of *Pseudogymnoascus appendiculatus*....................164

5.3. Light micrographs of *Pseudogymnoascus verrucosus*..........166

5.4. Scanning electron micrographs of *Pseudogymnoascus verrucosus*..........168

5.5. One of three most parsimonious trees from analysis of the ITS 1, 5.8S, and ITS 2 regions of the nuclear ribosomal DNA of *Pseudogymnoascus, Gymnostellatospora*, and *Geomyces* species and *Myxotrichum arcticum*..........170

6.1. Degradation of *Sphagnum* leaves by species of *Myxotrichaceae*. Decay resembles simultaneous white rot of wood..........190

6.2. Degradation of *Sphagnum* leaves by two white-rot basidiomycetes, *Bjerkandera adusta* and *Phanerochaete chrysosporium*. Decay resembles preferential white-rot of wood..........192

7.1. Morphology of *Oidiodendron maius* in axenic culture..........213

7.2. Degradation of *Sphagnum fuscum* leaf cell walls by *Oidiodendron maius*. Reproduced with permission from Tsuneda *et al.* 2001..........215

7.3. *Oidiodendron maius* (Hambleton personal collection, S-272a) colonizing the roots of *Vaccinium vitis-idaea*. Images provided by Sarah Hambleton..........217

CHAPTER 1: AN OVERVIEW OF THE *MYXOTRICHACEAE*, PEATLANDS, AND THE HISTORY OF *MYXOTRICHACEAE* IN PEAT

Climate change is among the world's most pressing environmental problems and its effects are predicted to be greatest in northern ecosystems. Peatlands, which currently store vast amounts of carbon (C), are considered to be among the most sensitive ecosystem types. Increased temperatures and decreased moisture associated with global warming are predicted to trigger a dramatic increase in decomposition rates in peatlands and a resultant release of C that may serve as a positive feedback mechanism. Thus, understanding of the decomposition dynamics of peatlands is critical to predict accurately the effects of climate change.

Peat decomposes slowly due to the combined effects of environmental factors, including low temperatures and pH and anoxia, and intrinsic characters, such as high concentrations of cellulose and phenolic compounds. An "enzymatic latch" mechanism (Freeman *et al.* 2001, Worrall *et al.* 2004) has been proposed to explain how global warming could trigger a catastrophic release of carbon from peatlands. In this scenario, increased temperatures and decreased moisture reduce the inhibition of enzymatic activity, particularly of phenol-oxidizing enzymes, causing an increase in aerobic decomposition. The decay of phenolic compounds, which inhibit the activity of many enzymes, would provide positive feedback, leading to even greater release of carbon (Freeman *et al.* 2001). However, this model does not incorporate the organisms that actually decompose peat. Relatively few fungi or bacteria produce phenol-oxidizing enzymes and the enzymes are present in relatively low concentrations in ecosystems. In fact, only about one quarter of the fungi isolated from peatlands by Thormann *et al.* (2001a, 2002) actually produced these enzymes. Therefore, in an attempt to reconcile these seemingly contradictory observations, I tried to isolate selectively phenol-oxidizing fungi from bog peat from the Perryvale Bog in Alberta, Canada. This site was selected because it has a history of fungal sampling and because there is a thick aerobic acrotelm where phenol-oxidase activity and the fungi that produce these enzymes should occur. Lignin-rich blocks of partially rotted wood were used to bait for phenol-oxidase producing fungi and growth media and moist chambers were used to selectively isolate basidiomycetes (the fungi that produce the most phenol-oxidases).

Contrary to my expectations, very few basidiomycetes were isolated from the bait blocks. Instead, the most common fungi from the blocks, and also from peat fragments harvested the previous summer, were ascomycetes, including representatives of the poorly known family *Myxotrichaceae*. Members of this family were the most common species on moist incubated peat fragments and bait blocks and on peat and bait placed on Mycosel® agar. These fungi are saprobes in soil and wood from temperate and colder regions of the world and some species may also form mycorrhizal associations. Their abundance in peat, relative to other substrates, combined with reports of their cellulolytic abilities, psychrophily and acidophily, suggested that they might be important in the carbon and nutrient cycling in peatlands and that their presence and activity in peatlands merited further attention.

The taxonomy and systematics of many of these species was uncertain and additional studies to clarify species relationships and identities were essential before accurate ecological assessments could be undertaken. The results of these taxonomic studies and ecological assessments are presented in later chapters. This chapter begins with an overview of the *Myxotrichaceae* and peatlands, then summarizes the results of previous studies on fungi, including *Myxotrichaceae*, in peatlands, and finally introduces the other chapters.

1.1. The *Myxotrichaceae* (*Ascomycota*)

The *Myxotrichaceae* includes three teleomorphic (sexual) genera, *Myxotrichum* Kunze [including *M. striatosporum* (Barron & Booth) Sigler (≡*Byssoascus striatisporus* (Barron & Booth) von Arx], *Pseudogymnoascus* Raillo, and *Gymnostellatospora* Udagawa, Uchiyama & Kamiya and their anamorphs, which are mostly in *Oidiodendron* Robak and *Geomyces* Traaen (Sigler *et al.* 2000). Most of the sexual species produce gymnothecial ascomata, globose asci, and hyaline to lightly pigmented, fusoid ascospores (Currah 1985, Sigler *et al.* 2000). Species vary in ascomatal complexity, from indistinct (*Gymnostellatospora subnuda* Sigler, Lumley & Currah) to the white telaperidium of *M. striatosporum*. Most species produce orange, red or dark brown reticuloperidia (Currah 1985, Sigler *et al.* 2000). Anamorphs, when present, are arthroconidial. Species of *Pseudogymnoascus* produce *Geomyces* anamorphs while the anamorphs of *Myxotrichum* species include simple, *Malbranchea* Saccardo-like arthroconidia and *Oidiodendron* species, and most *Gymnostellatospora* either lack anamorphs or produce scant *Ovadendron* Sigler & Carmichael- or *Malbranchea*-like conidia (Sigler *et al.* 2000).

1.1.1. Genera in the Myxotrichaceae

The three teleomorphic genera in the *Myxotrichaceae* can be distinguished by differences in ascospore ornamentation and ascomatal morphology (colour, appendages, texture of the peridial hyphae) and by their anamorphs. Most anamorphs are in the genera *Geomyces* and *Oidiodendron*. These genera can be distinguished based on conidiophore colour, conidial shape, and by the branching patterns of the conidiogenous hyphae.

1.1.1.1. *Myxotrichum*

Myxotrichum was described in 1823 (Kunze 1823, see Currah 1985). Ascospores of *Myxotrichum* species are hyaline to lightly pigmented, ellipsoidal to fusiform, and striate (Currah 1985, Sigler *et al.* 2000). Most of the approximately 15 species in this genus produce gymnothecia with dark brown peridial hyphae and elaborate appendages. Appendages may be straight and spine-like, curved at the apex, hooked, branched, unbranched, or deflexed (Currah 1985). The exception is *M. striatosporum*, which produces white telaperidia, although fascicular bundles of melanized, thick-walled hyphae are sometimes produced in culture (Sigler & Carmichael 1976, Currah 1985). Currah (1985) considered the telaperidium significant at the generic level, but subsequent molecular evidence (ribosomal DNA sequences) supports its inclusion in *Myxotrichum* (Hambleton *et al.* 1998) and it is treated herein as a species of *Myxotrichum* (Sigler & Carmichael 1976). A few *Myxotrichum* species lack anamorphs, but most produce arthroconidia assignable to either *Oidiodendron* or *Malbranchea* (Currah 1985). Only species of *Myxotrichum* with *Oidiodendron* anamorphs are included in this thesis.

Sterile peridial elements produced by *Oidiodendron maius* Barron are described and compared to the peridia of *Myxotrichum arcticum* Udagawa, Uchiyama & Kamiya ascomata in chapter 2. The *Oidiodendron* anamorphs of six *Myxotrichum* species are included in the keys in chapter 4 and three species are included in the Biolog analyses in chapter 3.

1.1.1.2. *Pseudogymnoascus*

Pseudogymnoascus was described in 1929 (Raillo 1929, Currah 1985). Ascospores are hyaline to lightly pigmented, ellipsoidal to fusiform, and smooth to irregularly ornamented. The type species, *P. roseus* Raillo, has smooth ascospores (Tsuneda 1982, Sigler *et al.* 2000), while *P. roseus* var. *ornatus* Udagawa & Uchiyama has ascospores with lobate-reticulate ornamentation (Udagawa & Uchiyama 1999). *Pseudogymnoascus appendiculatus* Rice & Currah, described in chapter 5, has ascospores with a faint longitudinal rim but are otherwise smooth, while *P. verrucosus* Rice & Currah, the second species described in chapter 5, has irregularly warty ascospores. Most species produce gymnothecia with red to red-brown, asperulate to warty, peridial hyphae, and short, subhyaline appendages. The exception is *P. appendiculatus*, which produces smooth-walled, orange peridial hyphae and long, branched, orange appendages. All species of *Pseudogymnoascus* produce aleurio- and arthroconidia in the genus *Geomyces*.

A phylogenetic analysis of *Pseudogymnoascus* and *Gymnostellatospora* (also in chapter 5) shows that the two genera are distinct. The abilities of the two new species to decompose *Sphagnum* and degrade cellulose and polyphenolics are discussed in chapter 6.

1.1.1.3. *Gymnostellatospora*

Udagawa *et al.* (1993) erected *Gymnostellatospora* to accommodate myxotrichoid species with crested ascospores. All seven species produce hyaline, ellipsoidal to fusiform ascospores with longitudinal ridges or striations ("crested" ascospores) and in most species, the ascospores also have a prominent longitudinal band or rim. Most species produce gymnothecia with yellow to yellow-brown or orange-brown peridial hyphae, with simple appendages. The appendages are typically shorter than 50 µm and are usually simple, hyaline to lightly pigmented, and unbranched but they may be straight or slightly curved. The exceptions are *G. subnuda* Sigler, Lumley & Currah and *G. parvula* Udagawa & Uchiyama, which have ascomata that lack distinct peridia (Sigler *et al.* 2000). Arthroconidial anamorphs have been reported for three species (Sigler *et al.* 2000) but conidia are usually scarce and simple and *Malbranchea*- or *Ovadendron*- like (Hambleton *et al.* 1998, Sigler *et al.* 2000).

The discovery of two species with characters intermediate between *Pseudogymnoascus* and *Gymnostellatospora* (i.e. ornamented ascospores and *Geomyces* anamorphs) prompted a phylogenetic analysis of the two genera based on the Internal Transcribed Spacer (ITS) 1, 5.8S, and ITS 2 regions of the nuclear rDNA. Results are included in chapter 5.

1.1.1.4. *Geomyces*

Geomyces was erected in 1914 for four species with different coloured colonies that produced aleurioconidia on erect, hyaline conidiophores (Sigler & Carmichael 1976). It was considered a synonym of *Chrysosporium* Corda (Carmichael 1962) but the two genera differ in conidiophore production, with *Geomyces* species producing conidia in verticillate whorls that are absent in *Chrysosporium* (Sigler & Carmichael 1976). Sigler and Carmichael (1976) recognized three species, including the anamorph of *P. roseus* but these were later considered varieties of *G. pannorum* (Link) Sigler & Carmichael (van Oorschot 1980) but molecular (chapter 5), morphological, and physiological (Plishka, unpublished) assessments indicate that the genus is polyphyletic and that there are complex relationships among isolates of the *G. pannorum* complex. *Geomyces* species produce small (<5 µm long) arthroconidia and aleurioconidia on acutely, verticillately branched, hyaline conidiophores (Sigler & Carmichael 1976). Arthroconidia are barrel-shaped to pyriform and aleurioconidia are pyriform. Colony colour varies in the genus, but may be white, yellow, or pink to purplish-red (Sigler & Carmichael 1976).

Geomyces species were among the most frequently encountered fungi in my isolations from Perryvale Bog (Chapter 6). Two new species with *Geomyces* anamorphs are described in Chapter 5 and isolates of *Geomyces* species are included in the phylogenetic analysis in that chapter. The abilities of selected isolates from the *Geomyces pannorum* complex to degrade cellulose and polyphenolic compounds and decompose *Sphagnum* L. are discussed in chapter 6.

1.1.1.5. *Oidiodendron*

Oidiodendron was erected in 1932 to accommodate arthroconidial species with melanized conidiophores and dichotomously branched, hyaline, fertile hyphae at their apices (Robak 1932). Most of the 23 species produce chains of small (<6 µm long), hyaline to melanized, unicellular arthroconidia through the basipetal fragmentation of fertile hyphae borne at the apices of solitary, erect, melanized conidiophores that are up to 500 µm long. Some species differ significantly from this pattern. *Oidiodendron myxotrichoides* Calduch, Gené & Guarro has a reticulate conidioma. Three species produce melanized, branched appendages at the conidiophore apex (Udagawa & Toyazaki 1987, Udagawa & Uchiyama 1998, Calduch *et al.* 2004). *Oidiodendron cerealis* (Thümen) Barron and the anamorph of *Myxotrichum setosum* (Eidam) Orr & Plunkett have short, hyaline to lightly melanized conidiophores, and thick-walled, melanized chlamydospores are produced by *O. chlamydosporicum* Morrall.

Oidiodendron maius, an ericoid mycorrhizal endophyte was the most frequently observed species on moist incubated peat (chapter 2) where it formed a sterile centrum surrounded by peridial elements that resembled the ascomata of *Myxotrichum arcticum* (chapter 2). The prevalence of this species as a saprobe in a bog with an understory dominated by its ericaceous hosts raised the question of its potential roles in this system: as a saprobe and as a mycorrhizal symbiont (chapter 7). Other species of *Oidiodendron* were isolated from Perryvale Bog or have been reported from peat. Morphological and physiological characters support the description of a new species of *Oidiodendron* originally isolated from mushroom compost (chapter 3) and are used in keys to 23 species in the genus (chapter 4). The abilities of the *Oidiodendron* species isolated from Perryvale Bog to degrade cellulose and polyphenolics and to decompose *Sphagnum* is discussed in chapter 6.

1.1.2. Taxonomic History

Myxotrichum and *Pseudogymnoascus* were formerly included in the family *Gymnoascaceae*, a family erected in 1872 to include ascomycete species that lacked a complete peridium enclosing the asci (Currah 1985). In 1893, the family was redefined to include simple, cleistothecial ascomycetes with a peridium of loosely differentiated hyphae surrounding the ascogenous tissue (Currah 1985) and *Myxotrichum* was included. Clements and Shear placed the family in the *Gymnascales* in 1931 and Benjamin added *Pseudogymnoascus* to the family in 1956 (Currah 1985). Although the family name *Myxotrichaceae* was proposed in 1974, it was not validly published until Currah (1985) erected it to include cellulolytic ascomycetes that produced small, lightly pigmented, fusoid ascospores in a gymnothecium (Currah 1985). He placed the family in the order *Onygenales*, which includes keratinolytic fungi and human pathogens, but indicated that it might be better accommodated elsewhere (Currah 1985, 1994). Udagawa *et al.* (1993) described the genus *Gymnostellatospora* and placed it in the *Myxotrichaceae*. Molecular evidence (Sugiyama *et al.* 1999, Mori *et al.* 2000, Gibas *et al.* 2002) and ascocarp development (Tsuneda & Currah 2004) indicate that the family should be included among the inoperculate discomycetes in the *Leotiomycetes*. Molecular evidence also indicates that there are two distinct lineages, one including *Myxotrichum* and its *Oidiodendron* anamorphs, the other including *Gymnostellatospora*, *Pseudogymnoascus* and anamorphs in *Geomyces* (Mori *et al.* 2000, Sigler *et al.* 2000).

1.1.3. Distribution, Occurrence and Ecology

Reports of the teleomorphic taxa in *Myxotrichaceae* are relatively rare (Currah 1985, Hambleton *et al.* 1998, Sigler *et al.* 2000) but most species are known from soil and decaying plant material, especially wood, in temperate and cool environments (e.g. Barron & Booth 1966, Udagawa *et al.* 1994, Udagawa & Uchiyama 1999, Sigler *et al.* 2000, Rice & Currah, in press 1) where their anamorphs may be abundant (e.g. Barron 1962, Morrall 1968, Sigler *et al.* 2000, Lumley *et al.* 2001, Rice & Currah, in press 1). For example, Sigler *et al.* (2000) isolated *Pseudogymnoascus roseus* and four *Gymnostellatospora* species from rotting wood in the boreal forest and Barron (1962) isolated nine species of *Oidiodendron* from peat and soil in Ontario. Species of *Geomyces* are among the most abundant fungi isolated from Antarctic and Arctic environments (e.g. Del Frate & Caretta 1990, Kerry 1990, Mercantini *et al.* 1993, Möller & Dreyfuss 1996, Azmi & Seppelt 1998, Marshall 1998, Sigler & Flis 1998, Bergero *et al.* 1999) and are common in other cold and temperate environments. They are also reported from insects (Greif, unpublished) and birds (Plishka, unpublished) in the boreal forest. There are also scattered reports of *Myxotrichaceae* from subtropical and tropical locations (e.g. Ellis 1971, Locquin-Linard 1982, Hambleton *et al.* 1998, Sigler & Flis 1998, Calduch *et al.* 2004, Roose-Amsaleg *et al.* 2004).

Most *Myxotrichaceae* are cellulolytic and many are psychrophilic or psychrotolerant (e.g. Currah 1985, Dalpé 1991, Uchiyama *et al.* 1995, Sigler *et al.* 2000, Udagawa & Uchiyama 2000, Tribe & Weber 2002, Rice & Currah, in press 1). Many species also produce other enzymes, including pectinases, amylases, lipases, gelatinases, chitinases, and polyphenoloxidases (e.g. Bending & Read 1996, 1997, Rice & Currah 2001, in press 1, Thormann *et al.* 2002) that potentially allow them to degrade a variety of plant, animal, and fungal-based substrates, including those found in wood, peat and soil (see chapters 4, 6). The ability of many *Myxotrichaceae* to grow at temperatures as low as 5°C, with optimal growth around 15-20°C and decreased growth at temperatures above 25°C may explain their prevalence in cool and temperate climates where average summer temperatures are below 25°C and their scarcity in warmer tropical and subtropical climates. Some *Myxotrichaceae*, notably many *Oidiodendron* species, are acidophilic and this predilection for acidic conditions may explain their abundance in peat (Barron 1962, Rice & Currah 2002, chapter 6) and the acidic soils of coniferous forests (e.g. Barron 1962, Morrall 1968, Gams & Söderström 1983).

In addition to the saprobic lifestyle, some species of *Oidiodendron* (e.g. Dalpé 1986, 1989, 1991, Currah *et al.* 1993) and *Pseudogymnoascus roseus* (Dalpé 1989) are known to form ericoid mycorrhizal associations *in vitro*. There are also reports of myxotrichoid fungi from ectomycorrhizal associations (Perotto *et al.* 1995, Sigler & Flis 1998, Bergero *et al.* 2000). Several species, including *Oidiodendron maius* var. *maius* (e.g. Couture *et al.* 1983, Schild *et al.* 1988, Douglas *et al.* 1989, Hambleton & Currah 1997, Qian *et al.* 1998), *O. maius* var. *citrinum* (Sigler & Flis 1998), and *P. roseus* (Currah 1985, Sigler & Flis 1998) have been isolated from the roots and rhizospheres of ericoid and ectomycorrhizal host plants. It is possible that these fungi also occupy a mycorrhizal niche in some habitats, including peatlands and coniferous forests. This relationship is facultative for the fungi, which often exist as free-living saprobes in the same environments (Rice & Currah, in press 2). The ability of these fungi to occupy both saprobic and mycorrhizal niches within the same environment may increase their importance in these ecosystems because the nutrients they liberate by decomposing the organic matter may be supplied directly and preferentially to their host plants (e.g. Northup *et al.* 1995, Aerts 2002, Leake *et al.* 2002).

Notably, the rotting wood, soil, peat, and other organic matter inhabited by members of the *Myxotrichaceae* are also attractive to insects. It has been hypothesized that the characteristic gymnothecia formed in this group, as well as their small, unicellular arthroconidia, and possibly the elaborate appendages and conidiomata formed in some *Oidiodendron* species, have evolved to facilitate insect dispersal within and between substrates (Currah 1985, 1994, Greif & Currah

2003). Greif and Currah (2003) found that gymnothecia could attach to insects as the insect hairs impale the ascocarp and may be carried for relatively long distances. It is possible that the appendages and conidiomata of some *Oidiodendron* species may play a similar role in attachment to insect vectors (Rice & Currah, in press 1). Greif and Currah (2003) also hypothesized that the small arthroconidia of the anamorphs could attach to insects via electrostatic forces for short-range dispersal.

Chapters 2, 6, and 7 discuss the distribution and potential ecology of myxotrichoid fungi that have been isolated from *Sphagnum* peat.

1.2. Peatlands

In most ecosystems, C uptake through photosynthesis is balanced by C release through decomposition. Peatlands are an exception. Peatlands are wetlands that have accumulated C over thousands of years because decomposition is much slower than production (e.g. Clymo 1965, Brinson *et al.* 1981, Farrish & Grigal 1988) and now store 20-30% of global soil C (Gorham 1991).

Despite their importance in global C storage, peatlands cover a relatively small percentage of the earth. Peatlands cover approximately 4% of the world's ice-free land area but about three quarters of this area is in northern countries. For example, peatlands cover about 14% of Canada's (National Wetlands Working Group 1988, Thormann, in press) and 16% of Alberta's land base (Vitt *et al.* 1996, Thormann *et al.* 2001a).

In Canada, there are five main types of peatlands distinguished by hydrological and vegetational characters: bogs, fens, marshes, swamps, and shallow open water (National Wetlands Working Group 1988, Thormann, in press). Of these, bogs and fens are the dominant peatland types in Canada and globally (Gorham 1991, Thormann, in press). Bogs form in wet areas where peat is domed above the water table and water, nutrients, and cations are supplied solely through the atmosphere (ombrotrophic) (Gorham 1991) and *Sphagnum* mosses tend to dominate the vegetation (e.g. Vitt 1994, Thormann, in press). In fens, water, nutrients, and cations are supplied both through the atmosphere and through ground water (minerotrophic) (Vitt 1994, Thormann, in press). Fens occur along a gradient of pH, nutrient concentrations, and vegetation but can be subdivided into two main types. Poor fens have low nutrient concentrations, are acidic, and their bryophyte cover is dominated by *Sphagnum*. Rich fens have higher nutrient concentrations and pH, and brown mosses are more common than *Sphagnum* (Vitt 1994, Thormann, in press).

Peatlands are expected to exhibit the greatest global warming induced changes because of their sensitivity to changes in seasonal temperature and water level fluctuations (Gignac *et al.* 1998). Because of their large C stores and potential to serve as either a source or a sink for the two most important greenhouse gases (carbon dioxide and methane), any process that alters the balance of C uptake and release from peatlands has potentially serious consequences for the global C cycle (e.g. Gorham 1991, Dunfield *et al.* 1993, Gignac *et al.* 1998, Roulet 2000). Interaction between temperature increase and water level decrease due to global warming is predicted to trigger a dramatic mobilization of peatland C (Gorham 1991, Freeman *et al.* 2001) because of increased aerobic decomposers (e.g. Gorham 1991, Zogg *et al.* 1997, Roulet 2000) and enzyme activity (Kang & Freeman 1994, Freeman *et al.* 2001). However, few studies that predict catastrophic mobilization of peatland C with global warming have looked at the effects of increased temperatures or carbon dioxide on the organisms responsible for peat decomposition, particularly fungi. One study that examined the effects of temperature on peat decomposition by fungi and bacteria, found that increased temperatures did not lead to uniform increases in decomposition (Thormann *et al.* 2004), indicating that caution and more research are needed to predict accurately the effects of global warming on peatlands.

1.2.1. Bogs

As mentioned in the previous section, bogs are ombrotrophic and form in wet areas where the peat is domed above the water table. Bogs cover approximately 5 % of Alberta (Vitt *et al.* 1996). In Canada, most bogs consist of a thick mat of *Sphagnum* mosses that form a series of hummocks and hollows. Many continental boreal bogs have a dense canopy of black spruce [*Picea mariana* (Miller) Britton, Sterns & Poggenburg] trees and an understory dominated by ericaceous shrubs, including *Vaccinium* L. species (e.g. bog cranberry and blueberry) and Labrador Tea [*Rhododendron groenlandicum* (Oeder) Kron & Judd] (e.g. Vitt *et al.* 1996). Bogs are acidic and their peat is preserved through the combined effects of low pH in the aerobic acrotelm and anaerobiosis in the catotelm as well as by intrinsic factors of the vegetation.

1.2.2. Decomposition of Sphagnum

Among peatland plants, *Sphagnum* is particularly resistant to decay and *Sphagnum*-dominated peatlands, including bogs, accumulate more C than any other peatland type (Verhoeven & Liefveld 1997). While environmental factors, including low temperatures, acidity, anoxia contribute to the slow decomposition of all bog plants, including *Sphagnum*, these mosses decompose slowly even in more favorable environments (Verhoeven & Liefveld 1997, Limpens

& Berendse 2003). Several intrinsic factors explain the recalcitrance of *Sphagnum* remains: high water-holding capacity and cation-exchange capacity, and the presence of inhibitory organic chemicals, including phenolics, uronic and other organic acids, and lipids in *Sphagnum* cells and cell walls. Like wood, *Sphagnum* leaf cell walls consist of a layer of cellulose fibrils bound by a protective, amorphous network of phenolic polymers and a lipid coating (Verhoeven & Liefveld 1997).

The abundance of phenolic polymers in *Sphagnum*-rich peat is particularly important in determining the slow decomposition of this material. Phenolic compounds, including tannins and lignin, accumulate in peat and may comprise up to 50% of its mass (Turetsky *et al.* 2000). Some of these compounds are byproducts of microbial decomposition (Dickinson 1979) while others are recalcitrant compounds from woody plants or *Sphagnum* (e.g. Verhoeven & Liefveld 1997, Tsuneda *et al.* 2001, Limpens & Berendse 2003). Phenolic compounds act as enzyme inhibitors, further slowing decomposition, which is already low due to low temperatures, acidity, and anoxia (Appel 1993, Bending & Read 1997). Anaerobic conditions and low temperatures currently prevailing in bogs limit the enzymatic breakdown of phenolic polymers (Pind *et al.* 1994) preventing decomposition. One of the mechanisms by which global warming may trigger a release of C from bogs is by increasing the breakdown of phenolics due to increased enzyme activity caused by warmer and drier conditions (Freeman *et al.* 2001). However, relatively few fungi in bogs produce the enzymes required to break down phenolics (Thormann *et al.* 2001a, 2002) and the effects of climate change on the distribution and activity of these fungi are unknown.

The potential of some *Myxotrichaceae* from peat to produce enzymes required to break down phenolic compounds and to decompose *Sphagnum* is explored in Chapter 6. These abilities are compared with those of two wood-decay ascomycetes and the process is compared with wood decay.

1.3. Fungi From Peatlands

Microfungal communities have been examined in the peatlands of Europe and North and South America (e.g. Boswell 1955, Christensen & Whittingham 1965, Dickinson & Dooley 1967, 1969, Christensen & Cook 1970, Dooley & Dickinson 1971, Dickinson 1979, Zattau 1981, Nilsson *et al.* 1992, Czeczuga 1993, Thormann *et al.* 2001a, see Thormann, in press for a review). Globally, there have been over 800 individual records of microfungi from peat, representing almost 650 different species (Thormann, in press). Over half (408) of these were anamorphic ascomycetes, 66 were zygomycetes, 20-30 each were chytrids, basidiomycetes, and teleomorphic ascomycetes, and about 100 were unidentified yeasts and sterile isolates of undetermined affinities (Thormann, in press).

Among anamorphic ascomycetes, fast-growing, prolific sporulaters in *Penicillium* Link and *Acremonium* Link are among the most frequently reported taxa. The eight most common genera (*Penicillium, Acremonium, Verticillium* Nees, *Aspergillus* Micheli *ex* Haller, *Trichoderma* Persoon, *Fusarium* Link, *Cladosporium* Link, and *Oidiodendron*) comprise almost half of all anamorphic ascomycete species isolated from peat (Thormann, in press).

Fungi are important saprobes in all ecosystems. Their extensive and rapid hyphal growth, and ability to translocate nutrients, acidophily, ability to degrade cellulose- and lignin-rich substrates, and a higher biomass and activity of fungi relative to bacteria in wetlands suggest that they are more important that bacteria in peat decomposition (e.g. Latter *et al.* 1967, Kuehn *et al.* 2000, Thormann, in press). Most of the fungi isolated from bogs (e.g. Christensen & Whittingham 1965, Dickinson & Dooley 1967, 1969, Christensen & Cook 1970, Nilsson *et al.* 1992, Thormann *et al.* 2001a, 2004) are saprobes (Thormann, in press). However, plant pathogens (Redhead 1981, Redhead & Spicer 1981, Tsuneda *et al.* 2000, Thormann *et al.* 2001b) and mycorrhizal fungi (e.g. Salo 1993, Dhillion 1994, Hambleton & Currah 1997, Hambleton *et al.* 1999, Thormann *et al.* 1999, Thormann *et al.* 2001a, Rice & Currah 2002) have also been reported from bogs.

Mycorrhizal fungi may be particularly important in nutrient cycling in peatlands. They are associated with the roots of many of the dominant plant species in bogs and fens (e.g. Wetzel & van der Valk 1996, Cooke & Lefor 1998, Thormann *et al.* 1999, Turner *et al.* 2000, Cornwell *et al.* 2001, Thormann, in press). Black spruce trees in bogs are ectomycorrhizal and their fruiting bodies can be abundant in peatlands (Salo 1993, Dhillion 1994, Thormann *et al.* 1999). The ericaceous shrubs that dominate the understory in bogs are all ericoid mycorrhizal (Hambleton & Currah 1997, Hambleton *et al.* 1999, Thormann *et al.* 1999). Ericoid mycorrhizal fungi are abundant in peat (e.g. Barron 1962, Rice & Currah 2002, in press 2) and may be able to use it as a C source (e.g. Tsuneda *et al.* 2001, Piercey *et al.* 2002, Thormann *et al.* 2002). Ectomycorrhizal fungi are able to use a variety of organic carbon and nitrogen sources, but most have limited abilities to use phenolic compounds (e.g. Hutchison 1990, 1991, Northup *et al.* 1995, Aerts 2002, Leake *et al.* 2002) and ericoid mycorrhizal fungi can break down organic C and nitrogen sources, including some phenolic compounds (Bending & Read 1996, 1997, Rice & Currah 2001, Aerts 2002). These fungi may be important in decomposition of peat and may preferentially supply their host plants with nutrients from these sources and reduce the amounts of nutrients available to other fungi and plants (e.g. Aerts 2002, Leake *et al.* 2002, Rice & Currah, in press 2).

1.4. *Myxotrichaceae* from peat

Previous reports of *Myxotrichaceae* from peat and peat soils concern *Oidiodendron* species (e.g. Barron 1962, Thormann *et al.* 2001a). Barron (1962) found that *Oidiodendron* species were common and among the dominant taxa in peat soils in Ontario. He reported seven *Oidiodendron* species from the peat soils of cedar- and cedar-birch bogs in Ontario: *O. cerealis*, *O. citrinum* Barron, *O. echinulatum* Barron, *O. flavum* von Szilvinyi, *O. maius*, *O. tenuissimum* (Peck) Hughes, and *O. truncatum* Barron (Barron 1962). Schild *et al.* (1988) found that *O. maius* was the most common sporulating fungus isolated from the roots of spruce trees from a blanket bog. Thormann *et al.* (2001) reported *O. maius* and *O. chlamydosporicum* from the *Sphagnum* peat of Perryvale Bog. Unlike Barron (1962) who found that *Oidiodendron* species were among the dominant peat-inhabiting fungi, Thormann *et al.* (2001) only recovered a single isolate of each of the two *Oidiodendron* species, possibly due to differences in isolation protocols. Unlike Thormann *et al.* (2001, 2004), I found myxotrichoid hyphomycetes, in *Oidiodendron* and *Geomyces*, to be among the most common fungi isolated from Perryvale Bog. I isolated six species of *Oidiodendron* from Perryvale Bog: *O. maius* (Chapters 2 and 6), *O. griseum* Robak, *O. periconioides* Morrall, *O. rhodogenum* Robak, and two unidentified species (Chapter 6) from Perryvale Bog, bringing to 13 the total number of *Oidiodendron* species isolated from peat. I am unaware of prior reports of *Geomyces* species or teleomorphic *Myxotrichaceae* from peat, but *Geomyces* has been isolated from bryophytes (e.g. Möller & Dreyfuss 1996) and it was one of the most common taxa isolated from Perryvale Bog (chapters 2, 6).

Chapters 2, 5, and 6 discuss the species of *Myxotrichaceae* isolated from Perryvale Bog and their abundance. Some of the discrepancy between my results and those of Thormann *et al.* (2001, 2004) is likely explained by differences in sampling protocols. The growth media used by Thormann *et al.* (2001, 2004) likely underestimate the abundance of these species in favour of faster-growing, heavily-sporulating species (Rice & Currah 2002). Moist chambers and Mycosel® agar favour the isolation of *Myxotrichaceae* (Rice & Currah 2002, chapter 6).

1.5. Taxonomic relationships among myxotrichaceous fungi

The first objective of this study was to examine the taxonomic relationships among myxotrichaceous fungi using a combination of morphological, physiological, and molecular methods. The use of morphological and physiological characters to distinguish species of

Oidiodendron is discussed in chapters 3 and 4. The use of morphological and molecular characters to distinguish two new species of *Pseudogymnoascus* and to provide a phylogenetic assessment of *Pseudogymnoascus* and *Gymnostellatospora* is presented in chapter 5.

1.6. Potential ecological roles of myxotrichaceous fungi in peat

The second objective of this study was to explore the possible ecological roles of *Myxotrichaceae* in peat using a series of physiological tests. The potential saprobic role of *Myxotrichaceae* in peat is presented in chapter 6. Chapter 7 discusses the potential of *Oidiodendron maius* to occupy both saprobic and mycorrhizal niches in peatlands and the potential importance of these dual roles. Chapter 8 discusses the major taxonomic and ecological conclusions and suggests avenues for future research.

1.7. Literature Cited

Aerts R (2002). The role of various types of mycorrhizal fungi in nutrient cycling and plant competition. In: van der Heijden MGA, Sanders IR (eds) *Ecological Studies, vol 157. Mycorrhizal Ecology*. Springer-Verlag, Berlin. pp. 117–133.

Appel HM (1993). Phenolics in ecological interactions: the importance of oxidation. *Journal of Chemical Ecology* **19**: 1521–1553.

Azmi OR, Seppelt RD (1998). The broad-scale distribution of microfungi in the Windmill Islands region, continental Antarctica. *Polar Biology* **19**: 92–100.

Barron GL (1962). New species and new records of *Oidiodendron. Canadian Journal of Botany* **40**: 589–607.

Barron GL, Booth C (1966). A new species of *Arachniotus* with an *Oidiodendron* conidial state. *Canadian Journal of Botany* **44**: 1057–1061.

Bending GD, Read DJ (1996). Nitrogen mobilization from tannin-protein complexes by ericoid and ectomycorrhizal fungi. *Soil Biology and Biochemistry* **28**: 1603–1612.

Bending GD, Read DJ (1997). Lignin and soluble phenolic degradation by ectomycorrhizal and ericoid mycorrhizal fungi. *Mycological Research* **101**: 1348–1354.

Bergero R, Girlanda MM, Varese GC, Intili D, Luppi AM (1999). Psychrooligotrophic fungi from Arctic soils of Franz Joseph Land. *Polar Biology* **21**: 361–368.

Bergero R, Perotto S, Girlanda MM, Vidano G, Luppi AM (2000). Ericoid mycorrhizal fungi are common root associates of a Mediterranean ectomycorrhizal plant (*Quercus ilex*). *Molecular Ecology* **9**: 1639–1649.

Boswell JG (1955). The microbiology of acid soils. IV. Selected sites in northern England and southern Scotland. *New Phytologist* **54**: 311–319.

Brinson MM, Lugo AE, Brown S (1981). Primary productivity, decomposition, and consumer activity in freshwater wetlands. *Annual Review of Ecology and Systematics* **12**: 123–161.

Calduch M, Gené J, Cano J, Stchigel A, Guarro J (2004). Three new species of *Oidiodendron* Robak from Spain. *Studies in Mycology* **50**: 159–170.

Carmichael JW (1962). *Chrysosporium* and some other aleurosporic hyphomycetes. *Canadian Journal of Botany* **40**: 1137–1173.

Christensen M, Whittingham WF (1965). The soil microfungi in open bogs and conifer swamps in Wisconsin. *Mycologia* **57**: 882–889.

Christensen PJ, Cook FD (1970). The microbiology of Alberta muskeg. *Canadian Journal of Soil Science* **50**: 171 – 178.

Clymo RS (1965). Experiments on the breakdown of *Sphagnum* in two bogs. *Journal of Ecology* **53**: 747–757.

Cooke JC, Lefor MW (1998). The mycorrhizal status of selected plant species from Connecticut wetlands and transition zones. *Restoration Ecology* **6**: 214–222.

Cornwell WK, Bedford BL, Chapin CT (2001). Occurrence of arbuscular mycorrhizal fungi in a phosphorus-poor wetland and mycorrhizal response to phosphorus fertilization. *American Journal of Botany* **88**: 1824–1829.

Couture M, Fortin JA, Dalpé Y (1983). *Oidiodendron griseum* Robak: an endophyte of ericoid mycorrhiza in *Vaccinium* spp. *New Phytologist* **95**: 375–380.

Currah RS (1985). Taxonomy of the *Onygenales*: *Arthrodermataceae, Gymnoascaceae, Myxotrichaceae* and *Onygenaceae*. *Mycotaxon* **24**: 1–216.

Currah RS (1994). Peridial morphology and evolution in the prototunicate ascomycetes. In: Hawksworth DL (ed) *Ascomycete Systematics: Problems and Perspectives in the Nineties*. Plenum Press, New York. pp 281–293.

Currah RS, Tsuneda A, Murakami S (1993). Conidiogenesis in *Oidiodendron periconioides* and ultrastructure of ericoid mycorrhizas formed with *Rhododendron brachycarpum*. *Canadian Journal of Botany* **71**: 1481–1485.

Czeczuga B (1993). Aquatic fungi of the Gorbacz and Ostrówski peatbogs. *Acta Mycologia* **28**: 69–75.

Dalpé Y (1986). Axenic synthesis of ericoid mycorrhiza in *Vaccinium angustifolium* Ait. by *Oidiodendron* species. *New Phytologist* **103**: 391–396.

Dalpé Y (1989). Ericoid mycorrhizal fungi in the *Myxotrichaceae* and *Gymnoascaceae*. *New Phytologist* **113**: 523–527.

Dalpé Y (1991). Statut endomycorrhizien du genre *Oidiodendron*. *Canadian Journal of Botany* **69**: 1712–1714.

Del Frate G, Caretta G (1990). Fungi isolated from Antarctic material. *Polar Biology* **11**: 1 – 7.

Dhillion SS (1994). Ectomycorrhizae, arbuscular mycorrhizae, and *Rhizoctonia* sp. of alpine and boreal *Salix* spp. in Norway. *Arctic and Alpine Research* **26**: 304–307.

Dickinson CH (1979). Microorganisms in peatlands. In: Gore AJP (ed) *Ecosystems of the World, 4A, Mires: Swamp, Bog, Fen, and Moor*. Elsevier, Amsterdam. pp. 225–243.

Dickinson CH, Dooley MJ (1967). The microbiology of cut-away peat. I. Descriptive ecology. *Plant and Soil* **27**: 172–186.

Dickinson CH, Dooley MJ (1969). Fungi associated with Irish peat bogs. *Proceedings of the Royal Irish Academy, Section B* **68**: 109–136.

Dooley M, Dickinson CH (1971). The ecology of fungi in peat. *Irish Journal of Agricultural Research* **10**: 195–206.

Douglas GC, Heslin MC, Reid C (1989). Isolation of *Oidiodendron maius* from *Rhododendron* and ultrastructural characteristics of synthesized mycorrhizas. *Canadian Journal of Botany* **67**: 2206–2212.

Dunfield P, Knowles R, Dumont R, Moore T (1993). Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. *Soil Biology and Biochemistry* **25**: 321–326.

Ellis MB (1971). *Dematiaceous Hyphomycetes*. Commonwealth Agricultural Bureaux, United Kingdom.

Farrish KW, Grigal DF (1988). Decomposition in an ombrotrophic bog and a minerotrophic fen in Minnesota. *Soil Science* **145**: 353–358.

Freeman C, Ostle N, Kang H (2001). An enzymatic 'latch' on a global carbon store. *Nature* **409**: 149.

Gams W, Söderström BE (1983). *Oidiodendron scytaloides* n. sp. *Cryptogamie, Mycologie* **4**: 239–243.

Gibas CFC, Sigler L, Summerbell RC, Currah RS (2002). Phylogeny of the genus *Arachnomyces* and its anamorphs and the establishment of *Arachnomycetales*, a new eurotiomycete order in the *Ascomycota*. *Studies in Mycology* **47**: 131–139.

Gignac LD, Nicholson BJ, Bayley SE (1998). The utilization of bryophytes in bioclimatic modeling: predicted northward migration of peatlands in the Mackenzie River Basin, Canada, as a result of global warming. *The Bryologist* **101**: 572–587.

Gorham E (1991). Northern peatlands: role in the carbon cycle and probable responses to global warming. *Ecological Applications* **1**: 182–195.

Greif MD, Currah RS (2003). A functional interpretation of the role of the reticuloperidium in whole-ascoma dispersal by arthropods. *Mycological Research* **107**: 77–81.

Hambleton S, Currah RS (1997). Fungal endophytes from the roots of alpine and boreal *Ericaceae*. *Canadian Journal of Botany* **75**: 1570–1581.

Hambleton S, Egger KN, Currah RS (1998). The genus *Oidiodendron*: species delimitation and phylogenetic relationships based on nuclear ribosomal DNA analysis. *Mycologia* **90**: 854–869.

Hambleton S, Huhtinen S, Currah RS (1999). *Hymenoscyphus ericae*: a new record from western Canada. *Mycological Research* **103**: 1391–1397.

Hutchison LJ (1990). Studies on the systematics of ectomycorrhizal fungi in axenic culture. II. The enzymatic degradation of selected carbon and nitrogen compounds. *Canadian Journal of Botany* **68**: 1522–1530.

Hutchison LJ (1991). Description and identification of cultures of ectomycorrhizal fungi found in North America. *Mycotaxon* **42**: 387–504.

Kang H, Freeman C (1994). Phosphatase and arylsulphatase activities in wetland soil: annual variation and controlling factors. *Soil Biology and Biochemistry* **31**: 449–454.

Kerry E (1990). Microorganisms colonizing plants and soils subjected to different degrees of human activity, including petroleum contamination, in the Vestfold Hills and MacRobertson Land, Antarctica. *Polar Biology* **10**: 423–430.

Kuehn KA, Lemke MJ, Suberkropp K, Wetzel RG (2000). Microbial biomass and production associated with decaying leaf litter of the emergent macrophyte *Juncus effusus*. *Limnology and Oceanography* **45**: 862–870.

Kunze G (1823). Einige neue odor verkannte Pilzattungen und Arten X. *Myxotrichum*. *Mykologische Hefte* **2**: 108–110.

Latter PM, Cragg JB, Heal OW (1967). Comparative studies of the microbiology of four moorland soils in the northern Pennines. *Journal of Ecology* **55**: 445–464.

Leake JR, Donnelly DP, Boddy L (2002). Interactions between ecto-mycorrhizal and saprotrophic fungi. In: van der Heijden MGA, Sanders IR (eds) *Ecological Studies, vol 157. Mycorrhizal Ecology*. Springer-Verlag, Berlin. pp. 345–372.

Limpens J, Berendse F (2003). How litter quality affects mass loss and N loss from decomposing *Sphagnum*. *Oikos* **103**: 537–547.

Locquin-Linard M (1982). *Pseudogymnoascus dendroideus* Locquin-Linard, nouvelle espèce de Gymnoascale (Ascomycètes) coprophile d'Afrique du Nord. *Cryptogamie, Mycologie* **3**: 409–414.

Lumley TC, Gignac LD, Currah RS (2001). Microfungus communities of white spruce and trembling aspen logs at different stages of decay in disturbed and undisturbed sites in the boreal mixedwood region of Alberta. *Canadian Journal of Botany* **79**: 76–92.

Marshall WA (1998). Aerial transport of keratinaceous substrate and distribution of the fungus *Geomyces pannorum* in Antarctic soils. *Microbial Ecology* **36**: 212–219.

Mercantini R, Marsella R, Moretto D, Finotti E (1993). Keratinophilic fungi in the Antarctic environment. *Mycopathologia* **122**: 169–175.

Möller C, Dreyfuss MM (1996). Microfungi from Antarctic lichens, mosses and vascular plants. *Mycologia* **88**: 922–933.

Mori Y, Sato Y, Takamatsu S (2000). Molecular phylogeny and radiation time of *Erysiphales* inferred from the nuclear ribosomal DNA sequences. *Mycoscience* **41**: 437–447.

Morrall RAA (1968). Two new species of *Oidiodendron* from boreal forest soils. *Canadian Journal of Botany* **46**: 203–206.

National Wetlands Working Group (1988). *Wetlands of Canada*. Ecological Land Classification Series, no. 24. Sustainable Development Branch, Environment Canada, Ottawa, ON and PolyScience Publications Inc., Montreal, PQ, Canada.

Nilsson M, Bååth E, Söderström B (1992). The microfungal communities of a mixed mire in Sweden. *Canadian Journal of Botany* **70**: 272–276.

Northup RR, Zengshou Y, Dahlgren RA, Vogt KA (1995). Polyphenol control of nitrogen release from pine litter. *Nature* **377**: 227–229.

Perotto S, Perotto R, Faccio A, Schubert A, Varma A, Bonfante P (1995). Ericoid mycorrhizal fungi: cellular and molecular bases of their interactions with the host plant. *Canadian Journal of Botany* **73**: S557–S568.

Piercey MM, Thormann MN, Currah RS (2002). Saprobic characteristics of three fungal taxa from ericalean roots and their association with the roots of *Rhododendron groenlandicum* and *Picea mariana* in culture. *Mycorrhiza* **12**: 175–180.

Pind A, Freeman C, Lock MA (1994). Enzymatic degradation of phenolic materials in peatlands – measurement of phenol oxidase activity. *Plant and Soil* **159**: 227–231.

Qian XM, El-Ashker A, Kottke I, Oberwinkler F (1998). Studies of pathogenic and antagonistic microfungal populations and their potential interactions in the mycorrhizoplane of Norway spruce [*Picea abies* (L.) Karst.] and beech (*Fagus sylvatica* L.) on acidified and limed plots. *Plant and Soil* **199**: 111–116.

Raillo A (1929). Beiträge zur Kenntis der Boden-Pilz. *Zentralblatt fur Bakteriologie und Parasitenkunde Jena Abth 2* **78**: 515–524.

Redhead SA (1981). Parasitism of bryophytes by agarics. *Canadian Journal of Botany* **59**: 63–67.

Redhead SA, Spicer KW (1981). *Discinella shimperi*, a circumpolar parasite of *Sphagnum squarrosum*, and notes on *Bryophytomyces sphagni*. *Mycologia* **73**: 904–913.

Rice AV, Currah RS (2001). Physiological and morphological variation in *Oidiodendron maius*. *Mycotaxon* **79**: 383–396.

Rice AV, Currah RS (2002). New perspectives on the niche and holomorph of the myxotrichoid hyphomycete, *Oidiodendron maius*. *Mycological Research* **106**: 1463–1467.

Rice AV, Currah RS (in press 1). *Oidiodendron*: A survey of the named species and related anamorphs of *Myxotrichum*. *Studies in Mycology* (accepted Feb. 2005).

Rice AV, Currah RS (in press 2). *Oidiodendron maius*: Saprobe in *Sphagnum* peat, mutualist in ericaceous roots? In: Schulz B, Boyle C, Sieber T (eds) *Microbial Root Endophytes*. Springer-Verlag, Heidelberg (Accepted Jan. 2005).

Robak H (1932). Investigations regarding fungi on Norwegian ground woodpulp and fungal infections at woodpulp mills. *Saertrykk av Nyt Magazin for Naturvidenskaberne* **71**: 185–330.

Roose-Amsaleg C, Brygoo Y, Harry M (2004). Ascomycete diversity in soil-feeding termite nests and soils from a tropical rainforest. *Environmental Microbiology* **6**: 462–469.

Roulet NT (2000). Peatlands, carbon storage, greenhouse gases, and the Kyoto Protocol: prospects and significance for Canada. *Wetlands* **20**: 605–615.

Salo K (1993). The composition and structure of macrofungus communities in boreal upland type forests and peatlands in North Karelia, Finland. *Karstenia* **33**: 61–99.

Schild DE, Kennedy A, Stuart MR (1988). Isolation of symbiont and associated fungi from ectomycorrhizas of Sitka spruce. *European Journal of Forest Pathology* **18**: 51–61.

Sigler L, Carmichael JW (1976). Taxonomy of *Malbranchea* and some other hyphomycetes with arthroconidia. *Mycotaxon* **4**: 349–488.

Sigler L, Flis A (1998). *Catalogue of the University of Alberta Microfungus Collections and Herbarium*, 3rd Edition. University of Alberta, Edmonton, AB, Canada. (available online at www.devonian.ualberta.ca/uamh)

Sigler L, Lumley TC, Currah RS (2000). New species and new records of saprophytic ascomycetes (*Myxotrichaceae*) from decaying logs in the boreal forest. *Mycoscience* **41**: 495–502.

Sugiyama S, Ohara A, Mikawa T (1999). Molecular phylogeny of onygenalean fungi based on small subunit ribosomal DNA (SSU rDNA) sequences. *Mycoscience* **40**: 251–258.

Thormann MN (in press). Diversity and function of fungi in peatlands: A carbon cycling perspective. *Canadian Journal of Soil Science*. (Accepted Mar. 2005).

Thormann MN, Bayley SE, Currah RS (2004). Microcosm tests of the effects of temperature and microbial species number on the decomposition of *Carex aquatilus* and *Sphagnum fuscum* litter from southern boreal peatlands. *Canadian Journal of Microbiology* **50**: 793–802.

Thormann MN, Currah RS, Bayley SE (1999). The mycorrhizal status of the dominant vegetation along a peatland gradient in southern boreal Alberta. *Wetlands* **19**: 438–450.

Thormann MN, Currah RS, Bayley SE (2001a). Microfungi isolated from *Sphagnum fuscum* from a southern boreal bog in Alberta. *The Bryologist* **104**: 548–559.

Thormann MN, Currah RS, Bayley SE (2002). The relative ability of fungi from *Sphagnum fuscum* to decompose selected carbon substrates. *Canadian Journal of Microbiology* **48**: 204–211.

Thormann MN, Currah RS, Bayley SE (2004). Patterns of distribution of microfungi in decomposing bog and fen plants. *Canadian Journal of Botany* **82**: 710–720.

Thormann MN, Myrholm CL, Mallett KI (2001b). *Armillaria sinapina* in herbaceous plant material from a peatland in Alberta, Canada. *Canadian Journal of Botany* **79**: 643–647.

Tribe HT, Weber RWS (2002). A low-temperature fungus from cardboard, *Myxotrichum chartarum*. *Mycologist* **16**: 3–5.

Tsuneda A (1982). Scanning electron microscopy of *Pseudogymnoascus roseus*. *Mycologia* **74**: 844–847.

Tsuneda A, Currah RS (2004). Ascomatal morphogenesis in *Myxotrichum arcticum* supports the derivation of the *Myxotrichaceae* from a discomycetous ancestor. *Mycologia* **96**: 627–635.

Tsuneda A, Thormann MN, Currah RS (2000). *Scleroconidioma*, a new genus of dematiaceous Hyphomycetes. *Canadian Journal of Botany* **78**: 1294–1298.

Tsuneda A, Thormann MN, Currah RS (2001). Modes of cell wall degradation of *Sphagnum fuscum* by *Acremonium* cf. *curvulum* and *Oidiodendron maius*. *Canadian Journal of Botany* **79**: 93–100.

Turetsky MR, Wieder RK, Williams CJ, Vitt DH (2000). Organic matter accumulation, peat chemistry, and permafrost melting in peatlands of boreal Alberta. *Écoscience* **7**: 379–392.

Turner SD, Amon JP, Schneble RM, Friese CF (2000). Mycorrhizal fungi associated with plants in ground-water fed wetlands. *Wetlands* **20**: 200–204.

Uchiyama S, Kamiya S, Udagawa S (1995). Five onygenalean fungi from Japan. *Mycoscience* **36**: 211–220.

Udagawa S, Toyazaki N (1987). A new species of *Oidiodendron*. *Mycotaxon* **28**: 233–240.

Udagawa S, Uchiyama S (1998). Three hyphomycetes isolated from soil and feather debris. *Canadian Journal of Botany* **76**: 1637–1646.

Udagawa S, Uchiyama S (1999). Taxonomic studies on new or critical fungi of non-pathogenic *Onygenales* 1. *Mycoscience* **40**: 277–290.

Udagawa S, Uchiyama S (2000). Two onygenalean fungi from Russian Far East soil. *Mycoscience* **41**: 217–221.

Udagawa S, Uchiyama S, Kamiya S (1993). *Gymnostellatospora*, a new genus of the *Myxotrichaceae*. *Mycotaxon* **48**: 157–164.

Udagawa S, Uchiyama S, Kamiya S (1994). A new species of *Myxotrichum* with an *Oidiodendron* anamorph. *Mycotaxon* **52**: 197–205.

Van Oorschot CAN (1980). A revision of *Chrysosporium* and allied genera. *Studies in Mycology* **20**: 1–89.

Verhoeven JTA, Liefveld WM (1997). The ecological significance of organochemical compounds in *Sphagnum*. *Acta Botanica Neerlandica* **46**: 117–130.

Vitt DH (1994). An overview of the factors that influence the development of Canadian peatlands. *Memoirs of the Entomological Society of Canada* **169**: 7–20.

Vitt DH, Halsey LA, Thormann MN, Martin T (1996). *Peatland Inventory of Alberta Phase 1: Overview of peatland resources in the natural regions and subregions of the province*. Alberta Peatland Resource Centre, Edmonton, AB, Canada. Publication 96-1.

Wetzel PR, van der Valk AG (1996). Vesicular-arbuscular mycorrhizae in prairie pothole vegetation in Iowa and North Dakota. *Canadian Journal of Botany* **74**: 883–890.

Worrall F, Burt T, Adamson J (2004). Can climate change explain increases in DOC flux from upland peat catchments? *Science of the Total Environment* **326**: 95–112.

Zattau WC (1981). Topographic features of chytrids collected from a *Sphagnum* bog. *Mycologia* **73**: 1189–1194.

Zogg GP, Zak DR, Ringelberg DB, MacDonald NW, Pregitzer KS, White DC (1997). Compositional and functional shifts in microbial communities due to soil warming. *Soil Science Society of America Journal* **61**: 475–481.

CHAPTER 2: NEW PERSPECTIVES ON THE NICHE AND HOLOMORPH OF THE MYXOTRICHOID HYPHOMYCETE, *OIDIODENDRON MAIUS*[1]

2.1. Introduction

Oidiodendron maius Barron is a widely distributed hyphomycete that has been isolated from a variety of substrates (e.g. Barron 1962, Lumley *et al.* 2001, Thormann *et al.* 2001) although most isolates are from the roots of ericaceous plants (e.g. Hambleton & Currah 1997, Hambleton *et al.* 1998, Monreal *et al.* 1999, Chambers *et al.* 2000). Consequently, it is often considered to have a niche similar to *Rhizoscyphus ericae* (Read) Zhuang & Korf [*Hymenoscyphus ericae* (Read) Korf & Kernan], an ascomycete well known as an ericoid mycorrhizal associate (Hambleton & Currah 1997, Monreal *et al.* 1999). *Oidiodendron maius*, like some other species of the genus, has been reported to form infection units in the roots of ericaceous plants (Douglas *et al.* 1989, Johansson 2001).

In *O. maius*, prolific sporulation, the production of a diverse suite of enzymes, and relatively rapid growth on a variety of culture media (Rice & Currah 2001) are characteristics suggesting a saprobic niche rather than a mycorrhizal one (Hutchison 1991). *In vitro*, *O. maius* is a proficient decomposer of *Sphagnum* L., the primary component of bog peat, causing significant mass losses (Piercey *et al.* 2002, Thormann *et al.* 2002) and degrading all cell wall components (Tsuneda *et al.* 2001). The species is also enzymatically diverse, degrading cellulose, pectin, and selected phenolic compounds (Rice & Currah 2001) that comprise a large proportion of peat (Turetsky *et al.* 2000).

Based on these observations, I hypothesized that *O. maius* is an abundant component of the saprobic microfungal community of bog peat and tested this by comparing several culturing methods for their efficacy in showing the presence of this species. In doing so, a sterile myxotrichoid 'gymnothecium' (Novák & Galgóczy 1965) was observed among stands of *O. maius* conidiophores on moist incubated peat. A series of crossing trials using a range of isolates showed that these sterile gymnothecia were relatively easy to induce under some conditions. Molecular analyses had indicated previously that the teleomorphs of *O. maius* should be expected in the genus *Myxotrichum* Kunze (Hambleton *et al.* 1998), but the distinctive gymnothecia typical of the genus remained unknown.

---

[1] A version of this chapter has been published: Rice AV, Currah RS (2002). New perspectives on the niche and holomorph of the myxotrichoid hyphomycete, *Oidiodendron maius*. *Mycological Research* **106**: 1463 – 1467.

This paper assesses the use of different culture techniques to determine the prevalence of *O. maius* in a series of peat samples and provides a description of the sterile myxotrichoid gymnothecia produced by this taxon.

2.2. Materials and Methods

2.2.1. Fungal Isolation

Peat samples were obtained (June-September) from three plots (minimum 2 m apart) within a *Sphagnum fuscum* (Schimp.) Klinggr.-*Picea mariana* (Miller) Britton, Sterns & Poggenburg (black spruce) bog (54° 28N, 113° 16W) near Perryvale in southern boreal Alberta ("Perryvale Bog"). The site was described by Thormann *et al.* (1999).

One 15 cm core (10 cm diam) was taken from the surface peat in each plot. Cores, consisting of a heterogeneous matrix of *Sphagnum*, spruce and ericaceous roots, and other debris, were cut into 2.5 cm thick cross sections, using a sterilized knife, and placed in sterile Petri plates for transport to the laboratory. Each cross section of peat was washed with sterile distilled water and divided into 10 smaller samples. Four fragments (5 cm x 5 cm x 0.5 cm) from each peat sample were placed into moist chambers, consisting of sterile plastic Petri plates lined with moist, sterile filter paper. Two fragments from each sample were cut into 30 5 x 5 mm segments, five of which were randomly selected for plating onto two replicate plates each of corn meal agar [CMA; 17.0 g Difco cornmeal agar (Difco Laboratories, Detroit, MI, USA), 1 l dH$_2$O], CMA with benomyl [CMAB; 17.0 g Difco cornmeal agar, 0.1 ml (1%) benomyl (Sigma Chemical Co., St. Louis, MO, USA) solution, 1 l dH$_2$O], and Mycobiotic® agar [MYCO; 35.6 g Difco Mycobiotic Agar (Difco), 1 l dH$_2$O]. Thus, 720 plates were prepared in total: 288 moist chambers, 144 CMA, 144 CMAB, 144 MYCO. All media were amended with oxytetracycline (0.02%) (Sigma) to control bacterial growth. Plates and moist chambers were incubated at room temperature in the dark for at least four months and monitored for fungal growth using dissecting and compound microscopes. Fungal identifications were based on morphological characters. Observed frequency for the most common sporulating species was based on the percentage of plates of each medium, including moist chambers, on or in which each taxon occurred. Differences in observational frequencies of the three most common taxa, i.e. *Mucor* Fresenius, *Penicillium* Link, and *Oidiodendron maius* were assessed using a series of χ^2 tests.

2.2.2. Crossing Trials

Because a sterile ascocarp was observed among conidiophores of *O. maius* on a peat fragment incubated in a moist chamber, I initiated a series of test crosses using 21 identified isolates of *O. maius* obtained from members of the Currah laboratory and the University of Alberta Microfungus Collection and Herbarium (UAMH) (described in Rice & Currah 2001; Table 2.1), including UAMH 9749, which was isolated from the Perryvale Bog (Thormann *et al.* 2001). Sterilized pieces of the fruticose thalli of a mixture of *Cladonia mitis* Sandstede and *C. rangiferina* (L.) Weber were placed in Petri plates with a basal layer of CMA, inoculated with all pairwise combinations of the 21 isolates, and incubated at room temperature in the dark. *Cladonia* L. was used as a substrate because at least one species of *Myxotrichum*, *M. bicolor* (Ehrenberg) Fries, forms extensive interconnected mats of gymnothecia on fruticose lichen thalli (Currah 1985), and *Cladonia* spp. are the most abundant fruticose lichens in Perryvale Bog. The fragments were monitored regularly for gymnothecia and these were examined using light microscopy.

2.3. Results and Discussion

2.3.1. Assessment of Oidiodendron maius *in bog peat*

Moist chambers are used to provide an accurate estimation of the fungal species that are active in some substrates (e.g. Bills & Polishook 1994, Richardson 2001) because plating on media is often biased toward the recovery of faster growing, highly sporulating species (Bissett & Widden 1972, Bills & Polishook 1994). Moist chambers are used regularly to study coprophilous fungi (Richardson 2001), but have been used rarely to sample the fungal community in soil or peat.

Oidiodendron maius was the most frequently observed species on peat incubated in the moist chambers, occurring in 99.6% of the chambers (Table 2.2) and growing readily on all components of the peat matrix. It is possible that washing the peat cross sections may have dispersed *O. maius* conidia throughout the *Sphagnum* matrix but presumably this heavier load of propagules would have yielded greater amounts of *O. maius* on the agar media along with a higher number of other heavily sporulating species on the moist incubated peat. It is impossible to determine conclusively whether the *O. maius* observed on the moist incubated peat was present in the original substrate as propagules or actively growing mycelia, but its ability to grow well on the natural substrate, under *in vitro* conditions, indicates that it has considerable potential to grow on this substrate *in situ*. Faster growing species, including *Mucor* spp. and *Penicillium* spp., were observed more rarely in the moist chambers than *O. maius* ($p<0.0001$) and were less abundant than on the agar media ($p<0.0005$) (Table 2.2). Notably, another myxotrichoid taxon, *Geomyces* Traaen, was more common on the moist incubated peat than non-myxotrichoid taxa. However, the statistical significance of this difference has not been calculated.

Conversely, species of *Mucor* and *Penicillium* overgrew plates of all three types of media and *O. maius* was more restricted. The selection of media may also bias the results of surveys (e.g. Lumley *et al.* 2000). Previous work has shown that *O. maius* grows and sporulates readily on CMA (Hambleton & Currah 1997, Rice & Currah 2001) but *O. maius* was observed on only 9% of the CMA plates (Table 2.2) and sporulated only on peat fragments on one-third of these plates. Benomyl favors the growth of basidiomycetes by discouraging the growth of many faster growing molds. *Oidiodendron maius* is an exception among these because it is tolerant of this compound; yet conidiophores of *O. maius* were observed on only one peat fragment on one CMAB plate (Table 2.2). Notably, species of *Mucor* were most abundant on CMAB plates while the *Penicillium* spp. occurred on over one fifth of them (Table 2.2). MYCO has been used previously to select for fungi with affinities to the *Onygenales*, *Microascaceae*, and *Myxotrichaceae*, including the sexual states of *Oidiodendron* species because these taxa are cycloheximide tolerant (Lumley *et al.* 2000). However, I did not observe asexual or sexual structures associated with *O. maius* on any MYCO plates (Table 2.2). *Geomyces* was the most frequently observed taxon on MYCO, being slightly more common than *Penicillium* species. The differences in observational frequencies among *Penicillium, Mucor*, and *Oidiodendron maius* on the three different isolation media are highly significant ($p<0.0001$).

While the widespread distribution of *O. maius* is recognized, it is considered uncommon except from the roots of ericaceous plants (Hambleton *et al.* 1998, Lacourt *et al.* 2001). *Oidiodendron maius* in other habitats or substrates may be overlooked by traditional sampling methods. It is not reported frequently from bryophyte substrates (Thormann *et al.* 2001) but my results indicate that *O. maius*, and other *Myxotrichaceae*, may be more common in bog peat than previously reported and that the isolation protocols used by most researchers may limit the recovery of *O. maius* from natural substrates.

2.3.2. Sterile myxotrichoid ascomata produced by Oidiodendron maius

After 1 month of incubation, a single sterile ascoma of an unknown *Myxotrichum* species developed among the conidiophores of *O. maius* on one moist incubated peat sample. A selection of *O. maius* isolates (18, including one from Perryvale Bog), grown in pairs on *Cladonia* thalli, yielded many similar, but also sterile, gymnothecial structures (Table 2.3). These data may indicate that *O. maius*, were it to form fertile gymnothecia, would be heterothallic; self-crosses never produced sterile gymnothecia. However, thallism remains a moot point because only four isolates, in combination with others, produced distinctive peridial elements and ascospores were absent from all of the gymnothecial structures.

The stimulatory effect of the *Cladonia* substrate on the production of sterile gymnothecia by paired *O. maius* isolates was striking. Previous studies with other arthroconidial taxa have shown that native substrate can be essential for the production of cleistothecia or cleistothecium-like structures (e.g. feathers as a keratin source for *Oncocladium*; Sigler *et al.* 1987). In this case, peridium formation, at least, could be dependent on the presence of fungal residues in the substrate; a feature that the moist incubated peat and the *Cladonia* thalli shared. The documented chitinolytic abilities of *O. maius* (Rice & Currah 2001) support this supposition.

The sterile gymnothecia (Figures 2.1A and 2.1B), produced singly or in clusters of 2-3 on the *Cladonia*, have a loose peridium of thick-walled, dematiaceous hyphae (2-6 µm thick). The peridial hyphae are smooth to asperulate with truncate to tapered ends (Figure 2.1B). In some instances, these structures resemble disorganized clusters of conidiophores but differ in that the conidiophores of *O. maius* are smooth, unbranched, and the pigmentation ends abruptly just before the conidiogenous apex. Many peridial hyphae are dichotomously branched with wide branch angles (Figure 2.1B). Appendages are absent.

Among the species described in *Myxotrichum*, the peridium is morphologically most similar to *M. arcticum* Udagawa, Uchiyama & Kamiya (Figures 2.1C and 2.1D). In *M. arcticum*, as in the sterile gymnothecia produced by *O. maius*, the thick-walled, darkly pigmented hyphae branch dichotomously and at broad angles (Figures 2.1B and 2.1D). *Myxotrichum arcticum* differs in that some peridial elements terminate in spine-like appendages (Udagawa *et al.* 1994). The *Oidiodendron* anamorph of *M. arcticum* is superficially similar to *O. maius* in bearing a cluster of pale arthroconidia at the tip of a tall, dematiaceous conidiophore. However, the anamorph of *M. arcticum* differs in having branched conidiophores and a geniculate fertile portion with short chains of conidia (Udagawa *et al.* 1994). The morphological similarities between *O. maius* and *M. arcticum* might indicate a close relationship between these two taxa but molecular evidence indicates that they are at least not conspecific (Hambleton *et al.* 1998). The production of sterile ascomata by *O. maius* provides additional evidence that the teleomorphs of *O. maius* belongs to the genus *Myxotrichum*.

Table 2.1. Location and collection sites for 21 isolates of *Oidiodendron maius* used in a series of controlled crosses established on sterilized thalli of *Cladonia* spp. Collectors are listed as footnotes

Isolate	Location
F-01[1]	*Empetrum nigrum*, birch dominated fjell, Kevo Research Station, Finland
F-02[1a]	*Vaccinium myrtillus*, birch dominated fjell, Kevo Research Station, Finland
F-03[1]	*V. vitis-idaea*, birch dominated fjell, Kevo Research Station, Finland
S1-P3-C-1[2]	*V. myrtilloides*, jack pine-aspen forest, 50 km S of Ft. McMurray, Canada
S1-P6-C-1[2a]	*V. myrtilloides*, jack pine-aspen forest, 50 km S of Ft. McMurray, Canada
S2-P3-C-1[2]	*V. myrtilloides*, jack pine-black spruce forest, Ft. McKay, Canada
S2-P6-P-9[2]	*V. myrtilloides*, jack pine-black spruce forest, Ft. McKay, Canada
S3-P6-M-1[2]	*V. myrtilloides*, jack pine-lichen hilltop, Ft. McKay, Canada
S4-P3-P-4[2a]	*V. myrtilloides*, disturbed sand hill, Ft. McKay, Canada
S4-P4-C-1[2]	*V. myrtilloides*, disturbed sand hill, Ft. McKay, Canada
S4-P6-C-1[2]	*V. myrtilloides*, disturbed sand hill, Ft. McKay, Canada
UAMH 1540[3]	Soil, cedar bog, Guelph, Canada; *ex*-type
UAMH 6514[4]	*Loiseleuria procumbens*, dry alpine ridge, Jasper National Park, Canada
UAMH 7022[5]	*Gaultheria shallon*, 3 yr old western hemlock stand, coastal BC, Canada
UAMH 8442[6]	*Rhododendron* sp., heath meadow, Ireland
UAMH 8529[7]	*V. corymbosum*, Quebec, Canada
UAMH 8920[8]	*Oxycoccus quadripetalus*, black spruce bog, AB, Canada
UAMH 8921[8]	*V. myrtilloides*, sand dune, AB, Canada
UAMH 8922[8]	*V. vitis-idaea*, sand dune, AB, Canada
UAMH 8933[9]	*Phyllodoce empetriformis*, alpine meadow, AB, Canada
UAMH 9749[10]	Decaying *Sphagnum fuscum*, Perryvale Bog, Canada

[1]Currah; [2]Hill-Rackette; [3]Barron; [4]Stoyke & Currah; [5]Xiao & Berch; [6]Douglas *et al.*; [7]Couture *et al.*; [8]Hambleton & Currah; [9]Hambleton; [10]Thormann.

[a]Later deposited at UAMH: F-02 = UAMH 10461; S4-P3-P-4 = UAMH 10460; S1-P6-C-1 = UAMH 10508

Table 2.2. Observational frequencies (expressed as % of plates with sporulating colonies) of *Oidiodendron maius* compared with *Geomyces, Penicillium* and *Mucor* (the three most common genera isolated from bog peat). MC = moist chambers, CMA = cornmeal agar, CMAB = cornmeal agar + benomyl, MYCO = mycobiotic agar.

Taxon	MC	CMA	CMAB	MYCO
Oidiodendron maius	99.6[a]***	9.0[c]**	0.7[c]**	0[c]**
Geomyces[N]	33.3	50.0	18.8	93.8
Mucor	27.8[b]**	94.4[d]	97.2[d]**	50.0[e]
Penicillium	14.6[b]**	94.4[d]*	22.2[b]*	91.0[d]**

[a] Significantly different from b and c ($p<0.0001$)

[b] Significantly different from a and d ($p<0.0001$) and e ($p<0.0005$)

[c] Significantly different from a, d, and e ($p<0.0001$)

[d] Significantly different from b and c ($p<0.0001$) and e ($p<0.0005$)

[e] Significantly different from c ($p<0.0001$) and d ($p<0.0005$)

* Significantly different from expected value: $0.0005<p<0.05$

** Highly significantly different from expected value: $p<0.0005$

*** Extremely significantly different from expected value: $p<0.0001$

[N] Data added later, not included in statistical analyses.

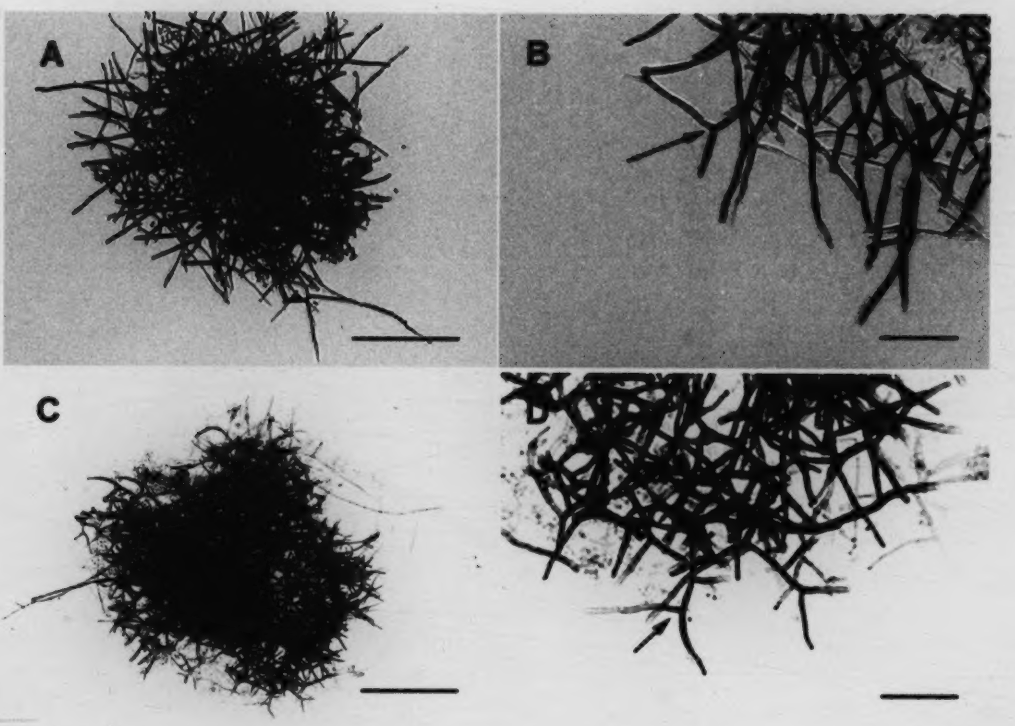
Table 2.3. Crosses among 18 isolates of *Oidiodendron maius* that produced sterile gymnothecia on sterilized *Cladonia* after 6 mo incubation. Crosses not yielding sterile gymnothecia are not shown). + = Sterile gymnothecia formed.

Isolate	S3-P6-M-1	S4-P3-P-4[a]	UAMH 8920	UAMH 8922
F-03	–	+	–	–
S1-P3-C-1	–	+	+	–
S1-P6-C-1[a]	+	+	+	–
S2-P3-C-1	–	+	–	–
S2-P6-P-9	+	+	–	–
S3-P6-M-1	–	+	+	–
S4-P3-P-4[a]	+	–	+	–
S4-P4-C-1	–	+	–	–
S4-P6-C-1	–	+	+	+
UAMH 1540	–	+	–	–
UAMH 6514	–	+	+	–
UAMH 7022	–	–	–	+
UAMH 8442	–	+	–	–
UAMH 8920	+	+	–	–
UAMH 8921	–	+	–	–
UAMH 8933	–	+	–	–
UAMH 9749	–	+	–	–

[a] Later deposited at UAMH: S1-P3-P-4 = UAMH 10460, S1-P6-C-1 = UAMH 10508

Figure 2.1. Sterile gymnothecia produced by *Oidiodendron maius* (UAMH 9749 crossed with UAMH 10460) after four months incubation on sterilized *Cladonia* (Figure 2.1A and 2.1B) and gymnothecia of *Myxotrichum arcticum* (UAMH 7565) (Figure 2.1C and 2.1D).

A. Sterile gymnothecium. Bar = 100 µm. **B**. Close up of peridial hyphae of sterile gymnothecium. Note dichotomous branches with wide branch angles (arrow) and the tapered apices of the peridial hyphae. Bar = 10 µm. **C**. Gymnothecium. This structure is morphologically similar to the sterile gymnothecia of *O. maius* (see **A**). Bar = 100 µm. **D**. Close up of peridial hyphae of the gymnothecium. Note dichotomous branches with wide branch angles (arrow) and tapered apices of the peridial hyphae. Bar = 20 µm.


A
B
C
D

2.4. Literature Cited

Barron GL (1962). New species and new records of *Oidiodendron*. *Canadian Journal of Botany* **40**: 589–607.

Bills GF, Polishook JD (1994). Abundance and diversity of microfungi in leaf litter of a lowland rain forest in Costa Rica. *Mycologia* **86**: 187–198.

Bissett J, Widden P (1972). An automatic, multichamber soil-washing apparatus for removing fungal spores from soil. *Canadian Journal of Microbiology* **18**: 1399–1404.

Chambers SM, Liu G, Cairney WG (2000). ITS rDNA sequence comparison of ericoid mycorrhizal endophytes from *Woollsia pungens*. *Mycological Research* **104**: 168–174.

Currah RS (1985). Taxonomy of the *Onygenales*: *Arthrodermataceae, Gymnoascaceae, Myxotrichaceae* and *Onygenaceae*. *Mycotaxon* **24**: 1–216.

Douglas GC, Heslin MC, Reid C (1989). Isolation of *Oidiodendron maius* from *Rhododendron* and ultrastructural characteristics of synthesized mycorrhizas. *Canadian Journal of Botany* **67**: 2206–2212.

Hambleton S, Currah RS (1997). Fungal endophytes from the roots of alpine and boreal *Ericaceae*. *Canadian Journal of Botany* **75**: 1570–1581.

Hambleton S, Egger KN, Currah RS (1998). The genus *Oidiodendron*: species delimitation and phylogenetic relationships based on nuclear ribosomal DNA analyses. *Mycologia* **90**: 854–869.

Hutchison LJ (1991). Description and identification of cultures of ectomycorrhizal fungi found in North America. *Mycotaxon* **42**: 387–504.

Johansson M (2001). Fungal associations of Danish *Calluna vulgaris* roots with special reference to ericoid mycorrhiza. *Plant and Soil* **231**: 225–232.

Lacourt I, Girlanda M, Perotto S, Del Paro M, Zuccon D, Luppi AM (2001). Nuclear ribosomal sequence analysis of *Oidiodendron*: towards a redefinition of ecologically relevant species. *New Phytologist* **149**: 565–576.

Lumley TC, Abbott SP, Currah RS (2000). Microscopic ascomycetes isolated from rotting wood in the boreal forest. *Mycotaxon* **74**: 395–414.

Lumley TC, Gignac LD, Currah RS (2001). Microfungus communities of white spruce and trembling aspen logs at different stages of decay in disturbed and undisturbed sites in the boreal mixedwood region of Alberta. *Canadian Journal of Botany* **79**: 76–92.

Monreal M, Berch SM, Berbee M (1999). Molecular diversity of ericoid mycorrhizal fungi. *Canadian Journal of Botany* **77**: 1580–1594.

Novák EK, Galgóczy J (1965) Notes on dermatophytes of soil origin. *Mycopathologia et Mycologia Applicata* **28**: 289–296.

Piercey MM, Thormann MN, Currah RS (2002). Saprobic characteristics of three fungal taxa from ericalean roots and their association with the roots of *Rhododendron groenlandicum* and *Picea mariana* in culture. *Mycorrhiza* **12**: 175–180.

Rice AV, Currah RS (2001). Physiological and morphological variation in *Oidiodendron maius*. *Mycotaxon* **79**: 383–396.

Richardson MJ (2001). Diversity and occurrence of coprophilous fungi. *Mycological Research* **105**: 387–402.

Sigler L, Guarro J, Currah RS, Punsola L (1987). Taxonomy of *Oncocladium flavum* and its relationship to *Malbranchea flava*. *Mycotaxon* **28**: 119–130.

Thormann MN, Currah RS, Bayley SE (1999). The mycorrhizal status of the dominant vegetation along a peatland gradient in southern boreal Alberta. *Wetlands* **19**: 438–450.

Thormann MN, Currah RS, Bayley SE (2001). Microfungi isolated from *Sphagnum fuscum* from a southern boreal bog in Alberta. *The Bryologist* **104**: 548–559.

Thormann MN, Currah RS, Bayley SE (2002). The relative ability of fungi from *Sphagnum fuscum* to decompose selected carbon substrates. *Canadian Journal of Microbiology* **48**: 204–211.

Tsuneda A, Thormann MN, Currah RS (2001). Modes of cell wall degradation of *Sphagnum fuscum* by *Acremonium* cf. *curvulum* and *Oidiodendron maius*. *Canadian Journal of Botany* **79**: 93–100.

Turetsky MR, Wieder RK, Williams CJ, Vitt DH (2000). Organic matter accumulation, peat chemistry, and permafrost melting in peatlands of boreal Alberta. *Écoscience* **7**: 379–392.

Udagawa S, Uchiyama S, Kamiya S (1994). A new species of *Myxotrichum* with an *Oidiodendron* anamorph. *Mycotaxon* **52**: 197–205.

CHAPTER 3: PROFILES FROM BIOLOG FF PLATES AND MORPHOLOGICAL CHARACTERISTICS SUPPORT THE RECOGNITION OF *OIDIODENDRON FIMICOLUM* SP. NOV.[2]

3.1. Introduction

In 1976, two isolates (DC 60, 61) of an undescribed *Oidiodendron* Robak species from mushroom compost were deposited as "*Oidiodendron* sp." in the culture collection of the Pennsylvania State Mushroom Spawn Laboratory, University Park, PA, USA. A putative subculture of DC 60, labeled "*Oidiodendron sindenia* Beyer" (Beyer pers. comm. 2002), was deposited as ATCC 36074 in the American Type Culture Collection (Manassas, VA, USA), but its accession data were lost, the culture later died, and the name was never published. Recently, I obtained cultures of DC 60 and 61 from the Pennsylvania State Mushroom Spawn Laboratory and recognized them as representing a hitherto undescribed species. The lost accession data and the resulting uncertainty concerning the relationship of these isolates to "*O. sindenia*", as listed in the ATCC database, prompted us to describe it under a new name.

Several morphological features associated with the new taxon are unique and probably sufficient on their own to justify recognizing it as distinct. Nonetheless, DNA evidence, which might support or challenge assumptions concerning its identity and placement among other species in *Oidiodendron*, was considered desirable. Repeated attempts to obtain DNA sequences were unsuccessful and, as a result, I used profiles obtained in the Biolog FF (filamentous fungal) physiological identification kit (Biolog Inc., Hayward, CA, USA) as a potential source of additional characters. *Oidiodendron* was not listed among the numerous hyphomycete genera in the Biolog fungal database and thus, for comparative purposes, I needed to generate substrate utilization profiles for a representative set of species.

In the present study, I provide a description of *Oidiodendron fimicolum* nom. prov. based on the two isolates mentioned above, and I compare its Biolog profile with those of 40 additional isolates representing 18 distinct taxa in either *Oidiodendron* or its teleomorphic counterpart, *Myxotrichum* Kunze.

---

[2] A version of this chapter has been accepted for publication: Rice AV, Currah RS (in press). Profiles from Biolog FF plates and morphological characters support the recognition of *Oidiodendron fimicolum* sp. nov. *Studies In Mycology* (accepted March 2005).

3.2. Materials and Methods

Isolates, including the *ex*-type culture and holotype specimen of *O. fimicolum*, are deposited at the University of Alberta Microfungus Collection and Herbarium (UAMH, Edmonton, AB, Canada), Centraalbureau voor Schimmelcultures (CBS, Utrecht, the Netherlands), or maintained by the author at the Department of Biological Sciences, University of Alberta (Edmonton, AB, Canada). Seven isolates with unknown or unconfirmed identities were included among the taxa studied.

Three replicates of each of the two isolates of the new species were grown as single-point-inoculated cultures on cornmeal agar [CMA; 15.0 g BBL cornmeal agar (Becton Dickinson Co., Sparks, MD, USA), 1 l dH_2O] and oatmeal agar [OA; 20.0 g Quaker oatmeal cereal, 20.0 g Bacto agar (Becton Dickinson Co.), 1 l dH_2O] at room temperature in the dark. Colonies were described and diameters measured at 28 days. Three slide cultures (Sigler & Flis 1998) of each isolate were mounted after 14 days incubation at room temperature in the dark. Conidia and conidiophores were measured and described according to Rice & Currah (in press). Dimensions were calculated from the mean of at least 10 measurements per slide per isolate. Observations were made using an Olympus BX 50 light microscope fitted with an Olympus DP 12 digital camera (Olympus Optical Co., Tokyo, Japan). Conidiophore and conidial ornamentation were observed using scanning electron microscopy (SEM). Mycelial plugs (2 mm x 2 mm) from sporulating cultures were freeze-dried in liquid nitrogen and examined using cryo-stage preparation in a JEOL #JSM6301FXV SEM (JEOL USA Inc., Peabody, MA, USA).

To obtain Biolog profiles, Biolog FF microplates were prepared for 42 isolates, representing 19 species (Table 3.1). Each isolate was first grown on five plates of 2% malt extract agar [MEA; 20.0 g malt extract (Becton Dickinson), 18.0 g Bacto agar, 1 l dH_2O] at room temperature in the dark so that sufficient quantities of conidia could be obtained for preparing conidial suspensions (see below). Isolates that failed to sporulate on MEA were grown on CMA or OA at room temperature in the dark. Seven isolates (UAMH 1405, 1523, 1525, 1540, 5715, 8511, 10464) were grown on OA plus either MEA or CMA; one isolate (UAMH 1399) was grown on all three media; and two replicates of each of three isolates (UAMH 1399, 1523, 5715) were grown on OA to test the amount of intra-isolate variability and the effect of growth media (see Table 3.1 for the number of Biolog FF plates prepared per isolate). After 35 days, conidia were collected with sterile cotton swabs. The swabs were dipped into screw-top culture tubes containing 16 ml Biolog FF inoculating fluid [2.5 g Phytagel (Sigma Chemical Co., St. Louis, MO, USA), 0.3 g TWEEN 40 (Sigma), 1 l dH_2O] and the mixture was vortexed briefly. The conidial suspension was prepared to 75% transmission as measured by a turbidimeter (Biolog) and 100 µl of suspension was pipetted into each of the 96 wells of a single Biolog FF plate. The resulting 54 Biolog plates were incubated at room temperature in the dark and read using a microplate reader (Biolog) at 1, 2, 3, 4, 7, and 10 days as suggested in the Biolog product information. Results were scored using 0 = no reaction, 1 = borderline positive reaction, and 2 = positive reaction (as indicated by the plate reader). The most consistent readings came from the 10-day-old Biolog plates and these were used in the analyses (below).

Data derived from study of all isolates were compared using the clustering program in PC-ORD (MjM Software, Gleneden Beach, OR, USA). Dendrograms were produced using seven linkage methods (nearest neighbour, farthest neighbour, group mean, median, centroid, McQuitty's method, and Ward's method) and seven distance measures (χ^2, Jaccard, Correlation, Euclidean, Relative Euclidean, Sorensen, and Relative Sorensen). Groups obtained in this manner were compared with distinctions among taxa based on morphological characters, simple substrate tests (Rice & Currah, in press), and ribosomal DNA (rDNA) sequences where available (Hambleton *et al.* 1998, Lacourt *et al.* 2001, Calduch *et al.* 2004, Sigler & Gibas, in press).

3.3. Results

3.3.1. Biolog

Each of the 54 Biolog FF data sets was unique. The cluster analysis computed using the linkage methods and distance measures given above yielded 37 different dendrograms. Dendrograms varied but five main clusters were generally consistent in approximately 80% of the topologies. A representative dendrogram is shown in Figure 3.1.

Intraspecific variation was considered low in *Oidiodendron fimicolum*, *O. rhodogenum* Robak, *Oidiodendron* sp. 1, and *O. truncatum* Barron because all tested isolates of these species were included in well-supported clusters (congruence among at least 80% of the dendrograms) that were only distantly connected to isolates of other species (Figure 3.1). Variation was moderate in *O. maius* Barron and *O. periconioides* Morrall, because some isolates of these species were included in well-supported clusters but others were outliers. Four of five isolates of *O. maius* formed a well-supported (81%) cluster while the fifth one (UAMH 9749) clustered most frequently with the *ex*-type of the morphologically similar anamorph of *Myxotrichum arcticum* Udagawa, Uchiyama & Kamiya. Two of the three *O. periconioides* isolates formed a well-supported (97%) cluster while the third (UAMH 8527) clustered with them in one dendrogram variant but remained isolated in other dendrograms. In *O. cerealis* (Thümen) Barron, variation was moderate: all three isolates clustered together in seven dendrograms (19%) and two or more isolates were together in 19 dendrograms (51%). Isolates of *O. cerealis* also clustered with *O. echinulatum* Barron in about half of the dendrograms.

Intraspecific variation was moderate to high in *O. griseum* Robak and *O. tenuissimum* (Peck) Hughes. Isolates of these species did not form distinct, well-supported clusters. Instead, they appeared in large clusters interspersed with members of other species. Isolates of *O. griseum* clustered with isolates of the related species *O. flavum* von Szilvinyi and *M. arcticum*, as well as with *O. setiferum* Udagawa & Toyazaki. *Oidiodendron tenuissimum* isolates clustered with those of *O. maius*, *O. chlamydosporicum* Morrall, and *M. arcticum*. Isolates of each of *M. arcticum, M. setosum* (Eidam) Orr & Plunkett, and *O. chlamydosporicum* never clustered together, indicating a high level of intraspecific variation in these taxa. Instead, the *ex*-type of *M. arcticum*, UAMH 7565, clustered with an isolate of *O. maius* var. *maius* in nine dendrograms, and with isolates of *O. tenuissimum* and *O. chlamydosporicum* in seven, while the second representative, UAMH 9243, clustered 92% of the time with isolates of *O. griseum*. One isolate of *M. setosum*, UAMH 3835, mainly clustered with the *ex*-type of *O. chlamydosporicum* (UAMH 6520; 57%) while the second test isolate, UAMH 4535, was distinct but was distantly connected with *O. fimicolum, M. cancellatum* Phillips, and one isolate of *O. tenuissimum* in seven dendrograms. In two dendrograms, it clustered with a second isolate of *O. chlamydosporicum*, UAMH 6521, and with *O. pilicola* Kobayasi. The third isolate of *O. chlamydosporicum*, UAMH 9751, formed a well-supported (73%) cluster with an isolate of *O. tenuissimum*, UAMH 8513.

In eight isolates tested in multiple replicate trials, each trial produced a distinct profile. The variation seen was low in *O. truncatum*, both in four replicates of UAMH 1399 and two replicates of UAMH 10464. The two replicates of UAMH 10464 differed from one another at seven wells and formed a distinct subgroup in all analyses, while the four replicates of UAMH 1399 differed at 23 wells and clustered together about 90% of the time. Replicate trials 'c' and 'd' of UAMH 1399, based on colonies grown on the same medium favoring conidial production, differed at 11 wells and were no more similar to each other than to replicates grown on different media. In *O. maius* the level of within-isolate variability was similar to levels of variability among isolates: replicates of the *ex*-type isolates of *O. maius* var. *maius* and *O. maius* Barron var. *citrinum* Rice & Currah were included in the same cluster, but were no closer to each other than to various other isolates. *Oidiodendron fuscum* Robak showed moderate-level variability, with two replicates of UAMH 8511 clustering together in over half the analyses. In *O. setiferum*, also rated moderately variable, UAMH 5715 replicates 'b' and 'c', grown on the same medium, clustered together in most analyses but grouped with replicate 'a' from a different medium only in somewhat more than one quarter of the analyses. Moderate variability was also seen in *O.*

tenuissimum. Variation was highest in *O. griseum*, where UAMH 1403 replicates 'a' and 'b' were part of the same cluster in less than half of the dendrograms. In many analyses, 'a' clustered with the *ex*-type of *O. flavum* while 'b' clustered with isolates of *O. griseum* and *M. arcticum*. *Oidiodendron echinulatum*, *O. flavum*, *O. pilicola*, *Oidiodendron* sp. 2, and *M. cancellatum*, each represented by a single test of a single isolate, were relatively distinct, showing distinct associations with isolates of other species in less than half of the analyses.

3.3.2. Taxonomy

Oidiodendron fimicolum Rice and Currah, **nom. prov.** Figure 3.2

Etym.: *fimus* refers to composted dung, a reference to the mushroom compost from which the *ex*-type was isolated.

Conidiophora 20-(50)-100 x 2-4 µm, non ramose vel dichotomose ramose, asperulata vel squamosa. Hyphae fertiles oriunt vel ab apicibus conidiophorum vel directe ab hyphis vegetativitis; erigunt catenas breves vel ramosas vel non ramosus arthroconidiorum. Conidia 3-(5)-6 x 2-(2.5)-3 µm, crassiter tunicata, asperulata, hyaline ad pallide-brunnea, dolioformia ad elongata vel irregularia et in extremis ambis truncata vel magis vel minus, inter se conexionibus distinctis separata. Isolatuma fimo ad cultum fungorum.

Holotypus: Colonia exsiccata ex UAMH 10459 *isolato ex fimo as cultum fungorum*, St. Louis, MO, USA.

Colonies on CMA 19-26 mm diam. at 28 days, off-white to beige or pale gray, appressed, with concentric rings of abundant conidiophores bearing masses of off-white to beige conidia; reverse olivaceous. Colonies on OA 20-22 mm diam. at 28 days, pale gray with olivaceous margins, appressed with concentric rings of abundant conidiophores bearing masses of off-white to gray conidia; reverse dark olivaceous to black. Conidiophores melanized, unbranched or dichotomously branched, 20-(50)-100 x 2-4 µm, appearing asperulate under light microscopy, covered in small scales visible in SEM. Fertile hyphae hyaline, 2-2.5 µm diam., arising from conidiophore apices or laterally from vegetative hyphae, fragmenting basipetally to form short, dichotomously- or sparsely- branched chains of arthroconidia. Conidia thick-walled, asperulate, hyaline to beige or pale brown, barrel-shaped to elongate or irregular, more or less truncate at one or both ends, 3-(5)-6 x 2-(2.5)-3 µm; connectives visible between conidia.

Holotype: Dried culture of isolate UAMH 10459 (specimen and *ex*-type culture share accession number) from mushroom compost, St. Louis, MO, USA. 1976, Beyer (= DC 60).

Additional Culture; **USA**, California, mushroom compost, 1976, Beyer (DC 61 = UAMH 10523)

3.4. Discussion

Oidiodendron fimicolum is most similar to *O. flavum* in producing irregularly shaped, lightly pigmented to melanized conidia, but it differs in having roughened rather than smooth conidiophores. The smooth to asperulate conidia of *O. fimicolum* and *O. flavum* are similar in light microscopy, but in SEM, the perispore can be seen to be slightly to markedly asperulate in *O. fimicolum*, while it is smooth to dimpled in *O. flavum*. In both species, conidial shape varies but the conidia of *O. fimicolum* are more or less ellipsoidal to elongate while those of *O. flavum* (Rice & Currah, in press) are subglobose to pyriform.

The two *O. fimicolum* isolates in Biolog FF plate profiles differed from one another only at eight wells. Five of these discrepancies involved wells that were either borderline positive or negative (scored as "0" or "1"), while the other three involved positive reactions differing in intensity (scored as "1" or "2"). These differences were of minimal import because the isolates clustered together with each other and remained relatively isolated from isolates of the other species in all of the 37 dendrograms calculated. In contrast to their superficial morphological similarities, *O. fimicolum* and an authentic isolate of *O. flavum* had markedly different Biolog profiles. They differed at 55 wells and did not cluster together in any dendrogram.

Relatively consistent topologies in Biolog-based dendrograms were also observed with the three isolates of *O. rhodogenum*, three isolates of *O. truncatum*, four isolates of *Oidiodendron* sp. 1, four of five test isolates of *O. maius*, and two of three isolates of *O. periconioides*: all formed distinct clusters in at least 80% of the dendrograms. With *O. truncatum*, all isolates clustered together consistently, including isolates from peat soils in Canada, mountain soil in Italy, and decaying wood in Canada. In *O. rhodogenum*, two isolates from *Sphagnum* L. peat in Canada clustered well with an isolate from Norwegian wood pulp. The two well-clustered isolates of *O. periconioides* both came from *Sphagnum* peat, while the single distinct isolate, the *ex*-type isolate, was from soil. It is possible that these physiological differences reflect different ecological adaptations. The varietal differences between *O. maius* var. *maius* and *O. maius* var. *citrinum* were not significantly reflected in Biolog FF profiles. The *ex*-type isolates of the two varieties clustered with each other while a second isolate of *O. maius* var. *maius* was an outlier.

The four isolates of *Oidiodendron* sp. 1 were all isolated from lignin bait blocks that had been set in the *Sphagnum* moss of a local bog. They may represent a new species. Morphologically, they are similar to *O. rhodogenum* but lack the characteristic diffusible red pigment and have conidia that are less heavily melanized. Both of these characters, however, can vary among *O. rhodogenum* isolates, and the new isolates could conceivably represent an ecological variant of this species. Consistent Biolog FF profiles for each set of representatives indicate that *Oidiodendron* sp. 1 might represent a distinct species but other criteria (e.g. DNA data) will be examined before a decision is made.

The groupings of *Oidiodendron* isolates based on Biolog FF profiles differ from groupings obtained in molecular studies (Hambleton *et al.* 1998, Lacourt *et al.* 2001, Calduch *et al.* 2004, Sigler & Gibas, in press). While the species that are distinct in Biolog analyses are also distinct in their relevant DNA sequences, where these have been done, the species that did not cluster well in Biolog tests have generally nonetheless been supported as distinct species in sequencing studies. Similarity in Biolog data is not expected necessarily to reflect phylogenetic relatedness, although some closely related species, including *O. flavum*, *O. griseum*, and *M. arcticum*, did cluster together in most of the analyses. Conversely, some species that clustered together in the Biolog data, such as *O. cerealis* and *O. echinulatum*, and *O. rhodogenum* and *O. periconioides*, are not closely related phylogenetically. Physiological profiles would be expected to show ecological or functional similarities or to reveal differences that would not have been disclosed by sequence analyses that adumbrated only a minute fraction of the genome. An example of functional similarity may be seen in the clustering of two *O. periconioides* isolates from peat with the isolates of *O. rhodogenum*, two of which are from the same peatland. Differences among isolates of individual species, for example in *O. maius*, *O. periconioides*, or *O. chlamydosporicum*, may indicate some ecological differentiation or adaptations for different habitats. Differences between or among replicates of the same isolate may be the result of heterokaryosis. The high level of physiological similarity noted between the two isolates of *O. fimicolum* may reflect their common adaptation to an unusual habitat, mushroom compost, as much as it reflects their intrinsic genetic similarity as conspecific isolates.

The use of Biolog profiles as ancillary taxonomic characters in the routine identification of *Oidiodendron* species can be recommended, but only with the caveat that the user must anticipate that in some cases, a very wide range of variation will occur among replicates and among conspecific isolates. Relatively few studies involving Biolog profiles of multiple isolates and sets of closely related species have been published (Wildman 1995, Talbot *et al.* 1996, Kubiček *et al.* 2003). Among conidial fungi, it may be typical to see high levels of variation in some species and low levels in others, as was observed here. Observations similar to ours have been made in examining Biolog profiles of collections of *Fusarium compactum* (Wollenw.) Gordon (Wildman 1995, Talbot *et al.* 1996) and *Trichoderma* Persoon (Kubiček *et al.* 2003) isolates. Before taxa are added to the Biolog database, screening multiple isolates (and replicates of these isolates) is necessary to allow quantification of the amount of variation that may occur. Also, such studies, interpreted in the light of phylogenetic studies, will reveal whether there are intraspecific patterns that might relate to ecological differences or to the differentiation of distinct subtaxa. Expansion of such studies would be particularly valuable for species like *O. maius* and *O. periconioides* where some isolates form distinct clusters but others appear to be outliers. Certainly, the species where only one isolate has been tested should be studied in more detail. Nevertheless, my preliminary evidence, albeit based on a limited data set, suggests that this method is promising as a source of additional characters for the definition of new species (e.g. *O. fimicolum*) and for the identification of species that seem to have relatively low levels of inherent variation (e.g. *O. rhodogenum* and *O. truncatum*).

Table 3.1. Isolate, species, collector, and collection information for isolates of *Oidiodendron* and *Myxotrichum* species used in the Biolog FF assessment.

Species	Isolate	Collector	Collection Information
M. arcticum	UAMH 7565[t]	Udagawa	Forest soil, USA
M. arcticum	UAMH 9243	Lumley	Decayed spruce, Canada
M. cancellatum	UAMH 1996	Udagawa	Soil, Japan
M. setosum	UAMH 3835	Bissett	Alpine soil, Canada
M. setosum	UAMH 4535	Bissett	Alpine soil, Canada
O. cerealis	CBS 349.62	Dal Vesco	Soil, Italy
O. cerealis	UAMH 504	Carmichael	Human hair, Canada
O. cerealis	UAMH 1522	Barron	Peat soil, Canada
O. chlamydosporicum	UAMH 6520[t]	Morrall	Forest soil, Canada
O. chlamydosporicum	UAMH 6521	Söderström, Bååth	Spruce humus, Sweden
O. chlamydosporicum	UAMH 9751	Thormann	*Sphagnum* bog, Canada
O. echinulatum	UAMH 8467[a]	Barron	Peat soil, Canada
O. fimicolum	UAMH 10459[t]	Beyer	Mushroom compost, USA
O. fimicolum	UAMH 10523	Beyer	Mushroom compost, USA
O. flavum	UAMH 1524	Barron	Peat soil, Canada
O. fuscum	UAMH 8511[t,2]	Robak	Wood pulp, Norway
O. griseum	UAMH 1403[a,2]	Melin	Wood pulp, Norway
O. griseum	UAMH 4080	Sigler	Wood chips, Canada
O. cf. *griseum*	DC 195	Davenport	Mushroom compost, USA
O. maius var. *citrinum*	UAMH 1525[t,2]	Barron	Cedar bog, Canada
O. maius var. *citrinum*	UAMH 7089	Malloch	Stream drift, Canada
O. maius var. *citrinum*	UAMH 9275	Hambleton	Ectomycorrhizal root, Canada
O. maius var. *maius*	UAMH 1540[t,2]	Barron	Peat soil, Canada
O. maius var. *maius*	UAMH 9749	Thormann	*Sphagnum* bog, Canada
O. periconioides	UAMH 8527[t]	Morrall	Forest soil, Canada
O. periconioides	UAMH 10463	Rice	*Sphagnum* bog, Canada
O. periconioides	UAMH 10522	Rice	*Sphagnum* bog, Canada
O. pilicola	UAMH 7526	Nylund	Forest soil, Sweden
O. rhodogenum	UAMH 1405[a]	Robak	Pulp sludge, Norway
O. rhodogenum	UAMH 10462	Rice	*Sphagnum* bog, Canada

O. rhodogenum	UAMH 10521	Rice	*Sphagnum* bog, Canada
O. setiferum	UAMH 5715[t,3]	Udagawa	House dust, Japan
O. tenuissimum	UAMH 1523[3]	Barron	Forest soil, Canada
O. tenuissimum	UAMH 8513	Castañeda	Leaf litter, Spain
O. truncatum	UAMH 1399[t,4]	Barron	Forest soil, Canada
O. truncatum	UAMH 8443	Mosca	Soil, Italy
O. truncatum	UAMH 10464[2]	Lumley	Decayed spruce, Canada
Oidiodendron sp. 1	2SMC1-1B	Rice	*Sphagnum* bog, Canada
Oidiodendron sp. 1	2SMC5-1A	Rice	*Sphagnum* bog, Canada
Oidiodendron sp. 1	3MMC3-7A	Rice	*Sphagnum* bog, Canada
Oidiodendron sp. 1	5JyMC2-5A	Rice	*Sphagnum* bog, Canada
Oidiodendron sp. 2	4SM3-3	Rice	*Sphagnum* bog, Canada

[a]Authentic, [t]*ex*-type culture, [2-4]Number of replicate Biolog plates (2, 3, or 4)

Figure 3.1. Representative dendrogram of 54 Biolog FF plate data sets for 42 isolates, representing 19 *Oidiodendron* and *Myxotrichum* species, produced using the Correlation distance measure and the Group Average linkage method. Note the well-supported clusters for *O. fimicolum, O. rhodogenum, O. truncatum, Oidiodendron* sp. 1, and most isolates of each of *O. maius* and *O. periconioides*. Bar = 25 % of information.

3.1

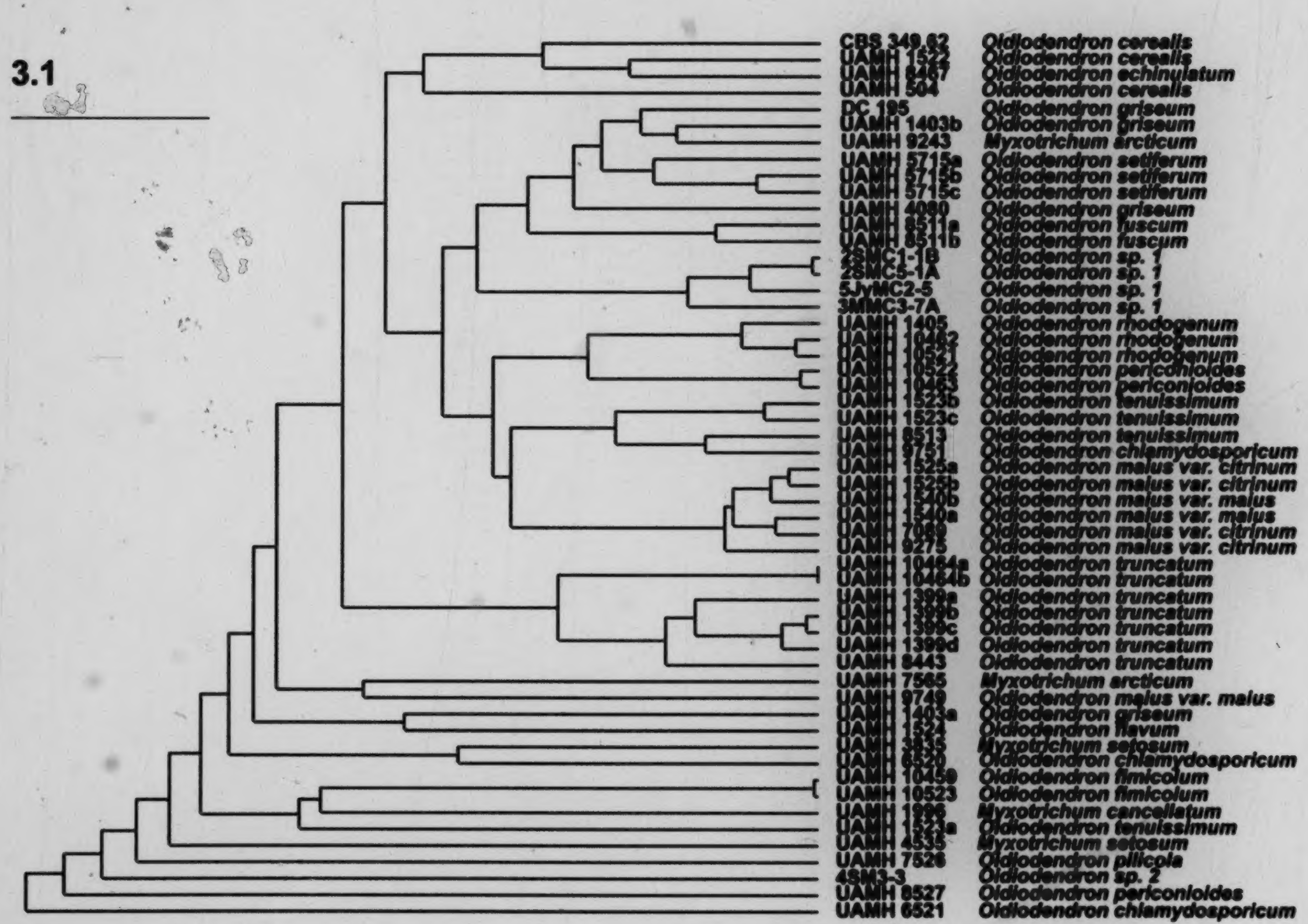
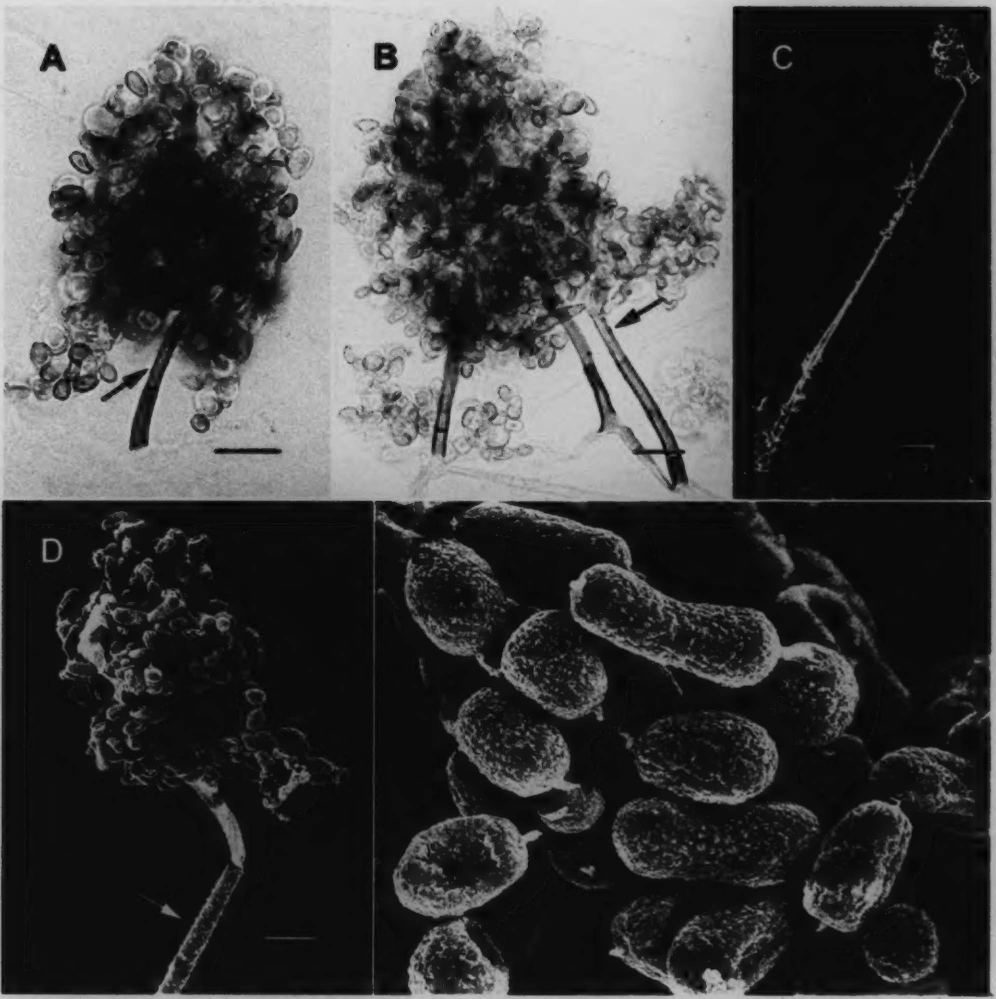

CBS 349.62 Oidiodendron cerealis
UAMH 1522 Oidiodendron cerealis
UAMH 8457 Oidiodendron echinulatum
UAMH 504 Oidiodendron cerealis
DC 195 Oidiodendron griseum
UAMH 1403b Oidiodendron griseum
UAMH 9243 Myxotrichum arcticum
UAMH 5715a Oidiodendron setiferum
UAMH 5715b Oidiodendron setiferum
UAMH 5715c Oidiodendron setiferum
UAMH 4080 Oidiodendron griseum
UAMH 8511a Oidiodendron fuscum
UAMH 8511b Oidiodendron fuscum
2SMC1-1B Oidiodendron sp. 1
2SMC5-1A Oidiodendron sp. 1
5JyMC2-5 Oidiodendron sp. 1
3MMC3-7A Oidiodendron sp. 1
UAMH 1405 Oidiodendron rhodogenum
UAMH 10462 Oidiodendron rhodogenum
UAMH 10521 Oidiodendron rhodogenum
UAMH 10522 Oidiodendron periconiolides
UAMH 10463 Oidiodendron periconioides
UAMH 1523b Oidiodendron tenuissimum
UAMH 1523c Oidiodendron tenuissimum
UAMH 8513 Oidiodendron tenuissimum
UAMH 9751 Oidiodendron chlamydosporicum
UAMH 1525a Oidiodendron malus var. citrinum
UAMH 1525b Oidiodendron malus var. citrinum
UAMH 1540b Oidiodendron malus var. malus
UAMH 1540a Oidiodendron malus var. malus
UAMH 7089 Oidiodendron malus var. citrinum
UAMH 9275 Oidiodendron malus var. citrinum
UAMH 10464a Oidiodendron truncatum
UAMH 10464b Oidiodendron truncatum
UAMH 1399a Oidiodendron truncatum
UAMH 1399b Oidiodendron truncatum
UAMH 1399c Oidiodendron truncatum
UAMH 1399d Oidiodendron truncatum
UAMH 8443 Oidiodendron truncatum
UAMH 7565 Myxotrichum arcticum
UAMH 9749 Oidiodendron malus var. malus
UAMH 1403a Oidiodendron griseum
UAMH 1524 Oidiodendron flavum
UAMH 3835 Myxotrichum setosum
UAMH 6520 Oidiodendron chlamydosporicum
UAMH 10459 Oidiodendron fimicolum
UAMH 10523 Oidiodendron fimicolum
UAMH 1996 Myxotrichum cancellatum
UAMH 1523a Oidiodendron tenuissimum
UAMH 4535 Myxotrichum setosum
UAMH 7526 Oidiodendron pilicola
4SM3-3 Oidiodendron sp. 2
UAMH 8527 Oidiodendron periconioides
UAMH 6521 Oidiodendron chlamydosporicum

Figure 3.2. Conidiophores and conidia of *O. fimicolum* Rice & Currah, sp. nov.

A. Mass of irregularly shaped, thick-walled, hyaline to melanized conidia produced at the apex of an asperulate conidiophore. Arrow indicates asperulate region. Bar = 15 µm. **B**. Asperulate (arrow) conidiophores bearing masses of irregularly shaped and pigmented conidiophores. Bar = 15 µm. **C**. Small, dense head of conidia at the apex of a solitary conidiophore. Bar = 10 µm. **D**. Dense head of irregularly shaped, asperulate conidia in chains at the conidiophore apex. Note the scales on the conidiophore (arrow) that give the conidiophores an asperulate appearance under light microscopy. Bar = 5 µm. **E**. Asperulate conidia. Note the varying shapes and sizes of the conidia and the connectives visible between them. Bar = 1 µm.


A
B
C
D

3.5. Literature Cited

Calduch M, Gené J, Cano J, Stchigel A, Guarro J (2004). Three new species of *Oidiodendron* Robak from Spain. *Studies in Mycology* **50**: 159–170.

Hambleton S, Egger KN, Currah RS (1998). The genus *Oidiodendron*: species delimitation and phylogenetic relationships based on nuclear ribosomal DNA analysis. *Mycologia* **90**: 854–869.

Kubiček CP, Bisset J, Druzhinina I, Kullnig-Gradinger C, Szakacs G (2003). Genetic and metabolic diversity of *Trichoderma*: A case study on South-East Asian isolates. *Fungal Genetics and Biology* **38**: 310–319.

Lacourt I, Girlanda M, Perotto S, Del Paro M, Zuccon D, Luppi AM (2001). Nuclear ribosomal sequence analysis of *Oidiodendron*: towards a redefinition of ecologically relevant species. *New Phytologist* **149**: 565–576.

Rice AV, Currah RS (in press). *Oidiodendron*: A survey of the named species and related anamorphs of *Myxotrichum*. *Studies in Mycology* (accepted February 2005).

Sigler L, Flis A (1998). *Catalogue of the University of Alberta Microfungus Collections and Herbarium*. 3rd Edition. University of Alberta, Edmonton, AB, Canada. 213 pp. (available online at www.devonian.ualberta.ca/uamh)

Sigler L, Gibas CFC (in press). Utility of a cultural method for identification of the ericoid mycobiont *Oidiodendron maius*. *Studies in Mycology*.

Talbot NJ, Vincent P, Wildman HG (1996). The influence of genotype and environment on the physiological and metabolic diversity of *Fusarium compactum*. *Fungal Genetics and Biology* **20**: 254–267.

Wildman HG (1995). Influence of habitat on the physiological and metabolic diversity of fungi. *Canadian Journal of Botany* **73**: S907–S916.

CHAPTER 4: *OIDIODENDRON*: A SURVEY OF THE NAMED SPECIES AND RELATED ANAMORPHS OF *MYXOTRICHUM*[3]

4.1. Introduction

Species of *Oidiodendron* Robak and the anamorphs of *Myxotrichum arcticum* Udagawa, Uchiyama & Kamiya, *M. cancellatum* Phillips, *M. emodense* Udagawa & Uchiyama, *M. setosum* (Eidam) Orr & Plunkett, and *M. striatosporum* (Barron & Booth) Sigler produce distinctive chains of small (<6 µm long), unicellular arthroconidia through the basipetal fragmentation of hyaline fertile hyphae. The fertile hyphae arise from the apices of solitary, erect, smooth to asperulate, melanized conidiophores that are 5-500 µm long but some species diverge significantly from this pattern. *Oidiodendron myxotrichoides* Calduch, Gené & Guarro produces fertile hyphae from the melanized branches of a reticulate conidioma. *Oidiodendron hughesii* Udagawa & Uchiyama, *O. muniellense* Calduch, Stchigel, Gené & Guarro, and *O. setiferum* Udagawa & Toyazaki have branched, melanized appendages surrounding the conidial mass at the conidiophore apices. *Oidiodendron cerealis* (Thümen) Barron and *M. setosum* have short, hyaline to lightly melanized conidiophores and *O. chlamydosporicum* Morrall has thick-walled, melanized chlamydospores. The anamorph of *M. arcticum* also produces whorls of conidia that occur singly and in truncated chains along the conidiophore apex.

Conidia may be hyaline to dark and are lens-shaped, globose to subglobose, ellipsoidal, elongated to cylindrical, barrel-shaped, pyriform, or irregular, and asperulate, verruculose, dimpled, rugose, spinulose, or reticulate. Scanning electron microscopy (SEM) shows that the characteristic surface ornamentation is due to the presence of a persistent perispore membrane derived from the wall of the conidiogenous hypha. Wall material from the conidiogenous hypha also persists between adjacent conidia where it eventually collapses to form "connectives" (Barron 1962).

Species of *Oidiodendron* have been isolated from soil, peat, humus, decaying wood, leaf litter, lichen thalli, roots, human hair and skin, and indoor and outdoor air samples, throughout temperate and northern ecosystems (e.g. Peyronel 1914, Robak 1932, Smith 1946, Malan 1949, Barron 1962, Morrall 1968, Kobayasi 1969, Udagawa & Toyazaki 1987, Hambleton *et al.* 1998, Sigler & Flis 1998). There are some reports from decaying organic matter in tropical and subtropical regions (Ellis 1971, Hambleton *et al.* 1998, Calduch *et al.* 2004, Roose-Amsaleg *et al.*

---

[3] A version of this chapter has been accepted for publication: Rice AV, Currah RS (in press). *Oidiodendron*: A survey of the named species and related anamorphs of *Myxotrichum*. *Studies in Mycology* (Accepted February 2005).

2004) and from marine Holothurians and sediments in the Sea of Japan (Pivkin 2000). Despite their widespread occurrence, there is no comprehensive key to the species of *Oidiodendron*. The keys in Barron (1962), Ellis (1971, 1976), Domsch *et al.* (1980) are out of date and rely exclusively on morphological characters. Calduch *et al.* (2004) included 23 species in a key but four are not well accommodated in *Oidiodendron*, three are synonyms of other species, and the unnamed anamorphs of *Myxotrichum* species are not included.

Because morphological characters alone are sometimes inadequate, I sought additional characters by investigating a suite of simple physiological tests. These have been incorporated into updated dichotomous and synoptic keys to 24 species or varieties. Preceding the keys is a review of the taxonomic history, distribution and ecology of the genus. Following a description of the procedures used to describe morphological and physiological characters is an assessment of their taxonomic value. Species descriptions follow the keys and are in alphabetical order.

4.1.1. Taxonomic History

The hyphomycete genus *Oidiodendron* was established by Robak (1932) for three species isolated from wood pulp: *O. fuscum* Robak, *O. nigrum* Robak, and *O. rhodogenum* Robak with *O. fuscum* as the type. I accept 24 species, including 18 species named in *Oidiodendron* and the unnamed anamorphs of five *Myxotrichum* Kunze species.

Four species were added to the genus over the next 30 years, including *O. griseum* Robak from wood pulp (Melin & Nannfeldt 1934) and *O. flavum* von Szilvinyi from soil (von Szilvinyi 1941). Two species were transferred into the genus: *Dicyma ambigua* Peyronel, the putative anamorph of *Myxotrichum aeruginosum* Mont. (Peyronel 1914, Malan 1949), as *O. ambiguum* (Peyronel) Malan (Malan 1949) and *Periconia tenuissima* Peck as *O. tenuissimum* (Peck) Hughes (Hughes 1958).

In 1962, Barron reviewed the genus, adding four new species, transferring a fifth species, and designating two pairs of synonyms. *Oidiodendron citrinum* Barron, *O. echinulatum* Barron, *O. maius* Barron, and *O. truncatum* Barron were all isolated from peat soils in Ontario. *Trichosporium cerealis* Thümen was transferred into *Oidiodendron*, as an earlier synonym of *O. nigrum*. He also considered *O. fuscum* synonymous with *O. tenuissimum* and designated it as the type of the genus. The first key to the genus appeared in this publication and included nine species: *O. cerealis, O. echinulatum, O. flavum, O. griseum, O. maius, O. rhodogenum, O. tenussimum,* and *O. truncatum* (Barron 1962). Hambleton *et al.* (1998), using ribosomal DNA sequences, determined that *O. tenuissimum sensu* Barron comprised two species. My morphological and physiological evidence indicate that these correspond to *O. fuscum* Robak and *O. tenuissimum* (Peck) Hughes. I, therefore, recommend reinstatement of the original type.

During the next eight years, six additional species were described. The first of these was *O. gracile* Zhadnova from the rhizosphere of maize (Zhadnova 1963) but Morrall (1968) designated it a *nomen dubium* because no type was declared and it was unclear from the original descriptions and figures whether the spores were arthroconidial or produced by acrogenous budding. Morrall (1968) also described *O. chlamydosporicum* and *O. periconioides* Morrall from boreal forest soils. Tewari and MacPherson (1968) described the *in vitro* neuropathology in mice of a species they later described as *O. kalrai* Tewari & MacPherson (Tewari & MacPherson 1971). However, this species was transferred to *Arthrographis* as *Arthrographis kalrae* (Tewari & MacPherson) Sigler & Carmichael on the basis of its hyaline conidiophores and smooth conidia that lack connectives (Sigler & Carmichael 1976). Two new species were described from soil in 1969, *Oidiodendron pilicola* Kobayasi based on an isolate on human hair (Kobayasi 1969) and *O. terrestre* Roy & Singh from India (Roy & Singh 1969). I exclude *O. terrestre* from *Oidiodendron* because of its rapid growth, large, two-celled conidia, hyaline conidiophores, and because of a lack of clarity about its mode of conidiogenesis in the original descriptions and illustrations.

Three species were proposed in the 1970s but two of these are probably synonyms of described species and the third was never validly published. Stalpers (1974) transferred *Oedocephalum sulphureum* Cooke & Massee into *Oidiodendron* as *O. sulphureum* (Cooke & Massee) Stalpers but was concerned that the species might be a synonym of *O. flavum*. I have not examined the type, no cultures are available, and Stalpers' brief descriptions and illustrations leave room for doubt. Further details are found under 'notes' following the description of *O. flavum*. Tokumasu (1973) and Söderström & Bååth (1978) isolated a species similar to *O. chlamydosporicum* from soil in Japan and Europe; it appeared as *O. scytaloides* in the key by Domsch *et al.* (1980) although it was not validly published as *O. scytaloides* Gams & Söderström until three years later (Gams & Söderström 1983). Molecular evidence (Hambleton *et al.* 1998, Calduch *et al.* 2004) and my examination of *ex*-type cultures of *O. scytaloides* and *O. chlamydosporicum* suggest they are synonyms. A culture of "*O. sindenia* Beyer", from mushroom compost, was deposited in the American Type Culture Collection (1976) but the name was not validly published (Beyer, pers. comm., 2002). Two cultures, one of them reportedly from the same collection, were obtained by the author, and are described as *O. fimicolum* Rice & Currah (Rice & Currah, in press 1).

Two species were described during the 1980s. The first, *O. robustum* Mercado Sierra & Castañeda Ruiz, from bark of *Bauhinia cumanensis* Kunth in Cuba (Mercado Sierra & Castañeda Ruiz 1985), is excluded based on the inordinately large conidia and conidiophores and on the lack of clarity in the descriptions and illustrations about the mode of conidiogenesis. *Oidiodendron setiferum* was described with branched, melanized appendages at the conidiophore apex and the genus was emended to accommodate this character (Udagawa & Toyazaki 1987).

From this point on, a succession of new species bearing these spiny or myxotrichoid appendages was described. A second species with melanized appendages, more elaborate than in *O. setiferum* and which form a "reticuloperidium-like" structure surrounding the arthroconidia, was named *O. hughesii* in 1998 (Udagawa & Uchiyama 1998). Calduch *et al.* (2002) described *O. myxotrichoides*, which produces arthroconidia on the melanized hyphae of a reticulate conidioma that superficially resembles the reticuloperidium of *Myxotrichum* ascomata. Calduch *et al.* (2004) described three more species with melanized appendages: *O. muniellense* with setiform appendages and subglobose, roughened conidia, *O. ramosum* Calduch, Stchigel, Gené & Guarro with recurved appendages and smooth to slightly roughened conidia, and *O. reticulatum* Calduch, Stchigel, Gené & Guarro with ellipsoidal, roughened conidia and appendages resembling those of *O. hughesii*. Comparisons of the original descriptions and illustrations of *O. hughesii, O. muniellense, O. ramosum,* and *O. reticulatum*, and *ex*-type material of *O. setiferum* suggest that *O. reticulatum* is a synonym of *O. hughesii* and *O. ramosum* is a synonym of *O. setiferum*.

In addition to the binomials in *Oidiodendron*, listed above, one named, and five unnamed species are components of holomorphs named in *Myxotrichum*. *Oidiodendron ambiguum* is listed as the anamorph of *M. aeruginosum* (Peyronel 1914, Malan 1949) and unnamed anamorphs are connected with *M. cancellatum* (Orr & Kuehn 1964), *M. setosum* (Orr *et al.* 1963), *M. striatosporum* [≡*Byssoascus striatosporus* (Barron & Booth) von Arx] (Barron & Booth 1966, Sigler & Carmichael 1976), *M. arcticum* (Udagawa *et al.* 1994), and *M. emodense* (Udagawa & Uchiyama 1999). In addition to these established anamorph-teleomorph connections, molecular evidence strongly supports the relationship between the species of *Oidiodendron* and teleomorphic taxa within the *Myxotrichaceae* (Hambleton *et al.* 1998). Molecular data (Sugiyama *et al.* 1999, Mori *et al.* 2000, Gibas *et al.* 2002) and a discomycetous type of ascocarp development in *M. arcticum* (Tsuneda & Currah 2004) also place the *Myxotrichaceae* among the inoperculate discomycetes (*Leotiomycetes*).

4.1.2. Distribution, Occurrence, and Ecology

Species of *Oidiodendron* are known as saprobes from a variety of living and decomposing plant, animal, and fungal substrates, including peat, soil, humus, wood, lichens, marine sediments and holothurians, and human skin and hair (e.g. Robak 1932, Smith 1946, Barron 1962, Morrall 1968, Kobayasi 1969, Domsch *et al.* 1980, Hambleton *et al.* 1998, Sigler & Flis 1998, Pivkin 2000, Lumley *et al.* 2001, Thormann *et al.* 2001, Rice & Currah 2002, Calduch *et al.* 2004). They have also been identified from human food supplies (Delamarre & Batt 1999, Krysińska-Traczyk *et al.* 2001) and indoor air and dust samples (Udagawa & Toyazaki 1987, Horak *et al.* 1996, Reiman & Uitti 2000). They occur throughout the temperate regions (e.g. Domsch *et al.* 1980, Hambleton *et al* 1998, Sigler & Flis 1998) and there are scattered reports from tropical and subtropical locales (Ellis 1971, Hambleton *et al.* 1998, Sigler & Flis 1998, Calduch *et al.* 2004, Roose-Amsaleg *et al.* 2004).

Oidiodendron maius Barron var. *maius* appears to form ericoid mycorrhizas with members of the *Ericaceae* in nature (Couture *et al.* 1983, Douglas *et al.* 1989, Hambleton & Currah 1997, Johansson 2001, Lacourt *et al.* 2001) and other species can produce morphologically similar structures *in vitro* (Dalpé 1986, 1989, 1991, Currah *et al.* 1993). This relationship is facultative for the fungi because they also persist as free-living saprobes in the same habitat (Tsuneda *et al.* 2001, Piercey *et al.* 2002, Rice & Currah 2002, in press 2).

Despite the reports of *Oidiodendron* species from a diverse array of substrates and environments, little is known about their ecological roles in nature. Most reports are incidental and indirect (e.g. Delamarre & Batt 1999, Pivkin 2000, Lumley *et al.* 2001, Roose-Amsaleg *et al.* 2004). Few researchers try to isolate *Oidiodendron* species specifically, and few speculate on their ecological roles (Rice & Currah 2002). The exception is *O. maius* var. *maius*, which is expected in and isolated deliberately from ericaceous roots in which a mutualistic role is presumed (Rice & Currah, in press 2). Most recent research on *Oidiodendron* has focused on the mycorrhizal status of the species and on the ecological significance of this association (e.g. Couture *et al.* 1983, Dalpé 1986, 1989, Douglas *et al.* 1989, Dalpé 1991, Currah *et al.* 1993, Perotto *et al.* 1995, Bending & Read 1997, Hambleton & Currah 1997, Currah *et al.* 1999, Xiao & Berch 1999, Piercey *et al.* 2002, Usuki *et al.* 2003). However, while benefits to the host plants have been observed in resynthesis studies, potential benefits to the mycobiont (*O. maius* var. *maius*) have not been investigated (Rice & Currah, in press 2). Ecological assessments have been further hampered by the inability to identify species accurately (Hambleton & Currah 1997, Hambleton *et al.* 1998, Lacourt *et al.* 2001). For example, misidentification of ericoid mycorrhizal isolates has led to difficulty in interpreting the specificity of these associations

(Hambleton & Currah 1997, Hambleton *et al.* 1998, Lacourt *et al.* 2001, Rice & Currah, in press 2).

Additional targeted isolation studies are required to determine which habitats and substrates are occupied by *Oidiodendron* species. These studies must be based on precise identifications so that estimations of the range, abundance, and distribution of *Oidiodendron* species in nature can be determined. Functional assessments, including enzyme assays and physiological profiles, mycorrhizal resynthesis and decomposition studies, and tests for pathogenicity are required to elucidate the niches occupied by these fungi. Data from the functional assessments and distribution data should be compiled to provide a more accurate picture of their ecology.

In vitro studies of the physiology of *Oidiodendron* species can provide insight into their potential ecological roles although they do not provide information about their actual ecological niches. Previous enzymatic studies of these species have concentrated on the ecological implications of their cellulolytic abilities (e.g. Dalpé 1991). While all but two of the tested species degraded cellulose azure, species of *Oidiodendron* produce various other enzymes, including pectinases, lipases, gelatinases, and polyphenol oxidases that potentially allow them to degrade a variety of plant, fungal, and animal-based substrates, including those found in soils. Broader substrate utilization profiles, including those generated by Biolog analyses (Rice & Currah, in press 1) could provide more information about their nutrition and potential ecological roles.

Five *Oidiodendron* or related *Myxotrichum* species (*M. cancellatum, M. setosum*, *O. hughesii, O. myxotrichoides*, and *O. truncatum*) are psychrophilic, with temperature optima below 20 °C. The remaining species are psychrotolerant, with temperature optima of 20-25 °C but able to grow at temperatures as low as 5 °C and displaying decreased growth at temperatures above 25 °C. These observations may explain the prevalence of *Oidiodendron* species in temperate climates, where average summer temperatures are below 25 °C, and their scarcity in warmer tropical and subtropical ecosystems. Most species of *Oidiodendron* are acidophilic with pH optima of 3-5; this predilection for acidic growth media may explain their abundance in peat (Barron 1962, Thormann *et al.* 2001, Rice & Currah 2002, Chapters 2 and 6) and the acidic soils of coniferous forests (e.g. Morrall 1968, Gams & Söderström 1983). The growth of *Oidiodendron* species in marine Holothurians and associated specimens (Pivkin 2000) is unusual but tolerance to relatively high salt concentrations does occur in some species (i.e. *O. maius* and *O. truncatum*, Rice & Currah 2001). The acidophilic nature and enzymatic abilities of ericoid mycorrhizal *Oidiodendron* species may partially explain the success of their host plants in acidic, nutrient-poor soils (Rice & Currah 2001, in press 2) and the higher pH optima and different enzymatic abilities of other *Oidiodendron* species may explain their failure to form either *in vitro* or *in situ* mycorrhizal associations. For example, *M. setosum* has a high pH optimum and is unable to utilize either cellulose or tannic acid. These attributes may partly explain its absence from *in situ* ericoid mycorrhizal associations even though it has been shown to form intracellular coils in these hosts *in vitro* (Dalpé 1989).

The predilection for cold, acidic environments rich in plant, animal, and fungal debris observed in many species of *Oidiodendron* may occur across the *Myxotrichaceae*. In addition to *Myxotrichum* and *Oidiodendron*, the family also includes *Gymnostellatospora, Pseudogymnoascus*, and the widespread anamorphic *Geomyces* (Currah 1985, Sigler *et al.* 2000). Species of *Geomyces* produce small, dry, unicellular, barrel-shaped to pyriform arthroconidia in dendritic clusters at the apices of erect, hyaline conidiophores (Sigler & Carmichael 1976). Species of *Gymnostellatospora, Myxotrichum*, and *Pseudogymnoascus* produce small, fusiform, hyaline to lightly pigmented ascospores in deliquescent, globose asci within reticuloperidia (Currah 1985, Sigler *et al.* 2000). Physiological requirements of most species of *Gymnostellatospora*, *Pseudogymnoascus*, and *Geomyces* are poorly studied, but there are reports of cellulolytic activity (Dalpé 1989, Udagawa *et al.* 1993, Uchiyama *et al.* 1995, Sigler *et al.* 2000, Udagawa & Uchiyama 2000) and psychrophily (Uchiyama *et al.* 1995, Sigler *et al.* 2000, Udagawa & Uchiyama 2000). Reports of the teleomorphic taxa are rare, but most species have been reported from decaying plant material and soils in temperate and cool environments (e.g. Udagawa *et al.* 1993, Uchiyama *et al.* 1995, Sigler *et al.* 2000, Udagawa & Uchiyama 2000) where their anamorphs may be common. *Myxotrichum chartarum* (Nees) Kunz lacks an anamorph but is also reported to be psychrophilic (Tribe & Weber 2002).

Myxotrichaceous fungi are common on decaying plant material that is attractive to insects. It has been suggested that the reticuloperidium of *Myxotrichaceae* is adapted for dispersal by arthropods (Currah 1985, 1994, Greif & Currah 2003) that may be facilitated by the passage of body hairs of insects or other arthropod carriers through the mesh-like peridium, thereby effectively attaching the ascocarp by ascocarp impalement (Greif & Currah 2003). Wind dispersal of the small, dry conidia of *Oidiodendron* and *Geomyces* is likely, but these conidia may also represent an adaptation for arthropod dispersal with conidia adhering to carriers by means of electrostatic forces (Greif & Currah 2003). Greif and Currah (2003) hypothesized that small arthropods may be most important in dispersing conidia locally while larger insects might disperse ascocarps over larger distances to fresh substrates. It is also possible that the reticulate conidiomata of *O. myxotrichoides* and the appendages of *O. hughesii*, *O. muniellense*, and *O. setiferum* may function in a similar manner by attaching masses of conidia to arthropod vectors.

4.2. Materials and Methods

Isolates were obtained from the University of Alberta Microfungus Collection and Herbarium (UAMH), Mushroom Spawn Laboratory, Pennsylvania State University (DC), and the Centraalbureau voor Schimmelcultures (CBS).

Information for some species was obtained solely from the literature. Living authentic or *ex*-type cultures of *O. ambiguum, O. hughesii, O. sulphureum, O. terrestre,* and *M. emodense* are not available from culture collections. *Oidiodendron muniellense, O. myxotrichoides, O. ramosum,* and *O. reticulatum* were published too close to the completion of this manuscript to be studied directly. Isolates of *O. pilicola* and *M. striatosporum* from UAMH had degenerated to a point that made morphological study unreliable. A permanent slide of the anamorph of *M. striatosporum* was obtained from UAMH and used for microscopic measurements and description.

4.2.1. Morphology

Three replicates each of 40 isolates (16 species, Table 4.1) were grown as single-point-inoculated cultures on plates of cornmeal agar with 0.01% oxytetracycline (Sigma Chemical Co., St. Louis, MO, USA) [CMA; 17 g Difco-Bacto cornmeal agar (Difco Laboratories, Detroit, MI, USA), 1 l dH_2O] at room temperature in the dark. Colonies were measured and described at 28 days. Colony texture and the abundance of aerial hyphae and conidiophores were noted. Colony colour was determined without reference to a colour standard.

Two separate slide cultures on 10% (w/v) cereal agar (Sigler & Flis 1998) of each isolate were mounted after 14 days incubation at room temperature in the dark. Conidiophore colour, texture, and branching pattern were recorded, as were conidial shape, colour, and surface ornamentation. Conidiophores were described as "branched" when conidium-bearing branches arose from the pigmented apical region of the conidiophore. Whether branches were dichotomous or trichotomous was also noted. Conidiophore length was measured from the point of origin to the end of the melanized portion. Mean conidiophore lengths and conidial dimensions were calculated using at least 10 randomly selected conidiophores or conidia from each slide culture. Measurements are given as minimum-(mean)-maximum. Appendages (n=10) of *O. setiferum* were measured from their origin on the conidiophore to the tip of the longest branch and the number per conidiophore was noted. Observations and measurements were made under oil immersion using an Olympus BX 50 light microscope (Olympus Optical Co., Tokyo, Japan). Photographs were made using an Olympus DP 12 digital camera (Olympus Optical Co.).

SEM images of conidia were prepared using mycelial plugs (5 mm x 5 mm) from five-week-old cultures on CMA. These were freeze-dried in liquid nitrogen and viewed on a cryo-stage in a JEOL #JSM6301FX7V SEM (JEOL USA Inc., Peabody, MA).

4.2.2. Physiological Studies

Thirty-eight isolates, representing 15 species, were used in the physiological tests (Table 4.1). Light, temperature, and pH tolerance tests follow Rice and Currah (2001). Unless otherwise stated, enzymatic assays follow Hutchison (1990) and Rice and Currah (2001). The effects of varied light, temperature, and pH used two replicates of each isolate grown on CMA under three light, six temperature, and five pH treatments. Growth rates were calculated using two independent measurements of colony radius of each replicate at 7, 14, 21, and 28 days. Growth rates (mm d^{-1}) of each isolate under each treatment were compared with growth rates under control conditions (CMA, room temperature, darkness).

Light treatments were diffuse daylight, darkness, and a black light (Philips F20T12-BL, 20 W; Philips Lighting, NJ, USA)-"growlight" (Sylvania F20T12, 20 W; Osram Sylvania, Mississauga, ON, Canada) regime ("black light") (Hambleton & Currah 1997, Rice & Currah 2001). Temperature treatments were 5, 10, 15, 20, 25, and 30 °C (± 1.5 °C). To determine the effect of pH, isolates were grown on CMA adjusted to pH 3, 5, 7, 9, and 11 using 1 N hydrochloric acid (HCl) and 10 % potassium hydroxide (KOH).

For enzyme assays, cultures were grown at room temperature in the dark on media containing the target macromolecule with or without an indicator.

Polyphenol oxidase (PPO) activity was assessed using tannic acid medium [TAM; 5 g tannic acid (BDH Inc., Toronto, ON, Canada), 200 ml dH_2O combined with 15 g Difco malt extract (Difco Laboratories), 20 g Difco-Bacto agar, 800 ml dH_2O after autoclaving] (Rice & Currah 2001) and wood guaiacol media [WDG; 2 g powdered wood (stem, *Picea glauca*, collected locally), 18 g Difco-Bacto agar, 100 µl guaiacol (Sigma) (added after autoclaving), 1 l dH_2O] (Miyamoto *et al.* 2000). Mycelial plugs (5 mm x 5 mm) were placed on plates of TAM and incubated for 48 hours. Darkening of the medium under the mycelial plugs indicates a positive reaction and the ability to degrade soluble phenolic polymers (Bending & Read 1997). Isolates were point-inoculated on plates of WDG and incubated for five weeks. Red discolouration of the medium around the mycelium indicates a positive reaction for the degradation of insoluble phenolic polymers, including lignin (Miyamoto *et al.* 2000).

Cellulases were detected using cellulose azure (Smith 1977, Hutchison 1990, Rice & Currah 2001). Modified Melin-Norkrans agar [MMN; 12 g Difco-Bacto agar, 3 g Difco malt extract, 1 g d-glucose anhydrous (Sigma), 1 g $CaCl_2$, 0.5 g NaCl, 10 g KH_2PO_4, 3 g $MgSO_4 \cdot 7H_2O$, 1 l dH_2O] (20 ml) was added to 50-ml Pyrex tubes, autoclaved, and allowed to solidify. A 2 % (w/v) solution of washed cellulose azure (Sigma) in MMN was autoclaved and 2 ml pipetted into each tube. Reactions were scored after five weeks based on the release of azure dye into the basal MMN layer.

Amylase activity was scored after isolates grew for three weeks on plates of MMN containing 2 g l^{-1} potato starch (BDH Inc., Poole, UK). Plates were flooded with iodine solution (5 g KI, 1.5 g I, 100 ml dH_2O) and decanted after several minutes to reveal a clear zone around the mycelium in strains positive for this enzyme.

Pectinase activity was determined after incubation for five weeks on MMN containing 5 g l^{-1} citrus pectin (Sigma). After plates were flooded for six hours with a 1 % (w/v) aqueous solution of hexadecylmethylammonium bromide (Sigma), a clear zone around the mycelium against an otherwise opaque background was interpreted as a positive indication of pectinase activity.

Gelatinase activity was indicated using MMN containing 60 g l^{-1} gelatin (Sigma) instead of agar. The gelatin was dissolved in 900 ml dH_2O and autoclaved, the remaining ingredients were autoclaved in 100 ml dH_2O, and the solutions were combined before pouring. Inoculated plates were incubated for a maximum of five weeks or until decomposition of the gelatin caused liquefaction of the medium.

Lipase synthesis was indicated using MMN containing 0.1 g l^{-1} $CaCl_2$ and 10 ml l^{-1} TWEEN 20 [polyoxyethylene sorbitan monolaurate (Sigma), added after autoclaving]. Isolates were incubated for 16 weeks and scored for the presence of macroscopically visible crystals of the calcium salt of the fatty acid beneath the mycelium.

4.3. Evaluation of Key Characters

4.3.1. Morphology

To date, keys to *Oidiodendron* species (Barron 1962, Ellis 1971, 1976, Domsch *et al.* 1980, Calduch *et al.* 2004) have been based exclusively on morphological characters, especially conidiophore length, conidial morphology, and cultural characteristics (Hambleton *et al.* 1998).

Conidiophores typically are erect and melanized and they branch at the apices to produce chains of arthroconidia. Conidiophore length, used regularly to delimit species, ranges from less than 5 to 500 µm. However, this character varies significantly among and even within conspecific isolates. For example, it ranged from 45 to 455 µm among 21 isolates of *O. maius* and from 123 to 455 µm within a single isolate (Rice & Currah 2001). Length ranges overlap among all species except *O. cerealis* (5-30 µm long) and *M. setosum* (typically <5 µm long) but it should be noted that conidiophores up to 140 µm long have been observed in *M. setosum* (Sigler & Carmichael 1976) and short, hyaline conidiophores do occur in other species. Consequently, the value of this character in identification is limited without consideration of other characters. Nonetheless, because conidiophore length is a readily observable character and because ranges are given in all species descriptions, I have incorporated these measurements into the dichotomous key. Users should be aware that this character is most useful when tendencies toward very short or very long conidiophores are considered in conjunction with other features.

Conidiophore branching, surface texture, and pigmentation are useful in some instances. Some species have conidiophores that do not branch within the melanized portion, while in others, dichotomous, and occasionally trichotomous, branching occurs. The conidiophores of most species are either consistently smooth or faintly and inconsistently asperulate, but those of *O. fimicolum* are scaly by SEM and asperulate by LM. *Oidiodendron cerealis* and *M. setosum* typically do not produce dark conidiophores; instead, conidiophores are short (typically <5 µm long in my observations of *M. setosum*, up to 30 µm long in *O. cerealis*), hyaline, and resemble vegetative hyphae. In other species, inconspicuous conidiophores are always accompanied by larger, melanized conidiophores.

"Connectives", the remains of the hyphal sleeve in which the conidia differentiate and which persist as collapsed wall material between mature conidia, are visible in many species. This character is not consistent within or among isolates and is not useful for distinguishing species. *Myxotrichum arcticum* also displays a unique form of conidiogenesis, termed "geniculate conidiogenesis", which results in the formation of truncated chains of one to two conidia borne in whorls at the conidiophore apex and perpendicular to the conidiophore axis (Udagawa *et al.* 1994, Tsuneda & Currah 2004). The ontogeny of these conidia is difficult to discern using light microscopy but the conidiophores that bear them terminate in a small, denser head of conidia that are not in chains, than the conidiophores that terminate in branched chains of arthroconidia.

Conidial size varies little among species and ranges from 1.5-3 x 1-2 µm to 3-7 x 2-4 µm. Most species produce conidia that range from 1.5-5 x 1-2.5 µm. Colour, shape, and ornamentation are variable but are consistent within species, and therefore are useful characters. Conidia may appear hyaline, lightly pigmented, or dark with the light microscope. This trichotomy is important in the keys. Conidial colour *en masse*, as determined using the dissecting microscope, varies from white to pale gray to green-gray, brown, or yellow and largely accounts for the characteristic colony colours.

Rice and Currah (2001) found that conidial ornamentation was consistent among 21 isolates of *O. maius* but distinct from that of a superficially similar isolate of *O. truncatum*. This character provided a clearer distinction between these species than did conidiophore length and conidial size. Other species also have distinctive conidial surfaces. For example, the conidia of *O. cerealis* are lens-shaped with a thickened ring and have a rugose (wrinkled) perispore. Conidia of *O. pilicola, O. truncatum, M. cancellatum*, and *M. striatosporum* are all barrel-shaped with truncate ends but differ in surface ornamentation. In *O. truncatum* and *M. cancellatum*, conidia have a wrinkled, net-like perispore (resulting in characteristic "reticulate ornamentation") while those of *O. pilicola* are smooth to minutely asperulate and *M. striatosporum* are asperulate. *Oidiodendron ambiguum, O. echinulatum,* and *O. periconioides*, all with subglobose to ellipsoidal conidia, differ in that the conidia of *O. ambiguum* have rounded and minutely verruculose (warty) surface projections, while those of *O. echinulatum* have larger, but still rounded (warty) projections, and *O. periconioides* have pointed and spinulose projections. The morphologically similar *O. muniellense* and *O. setiferum* can be distinguished by the ornamentation of their conidia, which is asperulate to spinulose in *O. muniellense* and smooth to reticulate in *O. setiferum*. Conidia of other species may be only slightly asperulate, reticulate, warty or dimpled by SEM and look smooth, or nearly so, by light microscopy. *Oidiodendron flavum* and *O. fimicolum* produce a variety of conidial shapes with smooth to asperulate ornamentation that differs significantly only under SEM. Conidial shapes are illustrated in Table 4.2.

Unique features, such as chlamydospores in *O. chlamydosporicum* and melanized appendages at the conidiophore apices of *O. muniellense, O. setiferum*, and *O. hughesii*, and making up the peridium-like enclosure on the sessile conidiomata in *O. myxotrichoides*, are useful characters. The appendages of *O. hughesii* are larger and more highly branched and complex than those of *O. muniellense* and *O. setiferum*, but are similar to those of *O. myxotrichoides* in forming a peridium-like structure surrounding the arthroconidia. In *O. hughesii* the peridium-like branches are borne on the conidiophore apex and do not form a sessile, ascocarp-like conidioma.

Colonial morphology, especially colour and the production of diffusible pigments and exudates, has also been used as a source of characters but can vary with growth medium and within isolates of the same species. Cultural characteristics are used in the keys only when they were reasonably consistent and are not used in isolation for distinguishing species. Sigler and Gibas (in press) report a culture-based method for distinguishing *O. maius* from other species.

4.3.2. Physiology

Physiological characters, including enzyme profiles and tolerance of different growth conditions, have seldom been used to distinguish among species in this genus (Rice & Currah 2001) but some appear to have discriminating value and are used in the dichotomous key where appropriate and in the species descriptions and synoptic key. These characters are presented with the caveat that only a small number (1-5) of isolates were tested to obtain profiles, which may underestimate the amount of variation for each character within species and across the genus.

Neither light nor temperature preferences discriminated among most species but some minor distinctions are noted. For example, the growth of *O. echinulatum* was suppressed by daylight. *Oidiodendron setiferum* grew optimally at 25 °C and *O. truncatum, M. cancellatum,* and *M. setosum* grew optimally below 20 °C, with growth suppressed at 25 °C. All others tested grew optimally at 20 °C. *Oidiodendron hughesii* and *O. myxotrichoides* were not tested here but were described as psychrophilic, with optimal growth at 15 °C (Udagawa & Uchiyama 1998, Calduch *et al.* 2002), *O. muniellense* grows optimally at 25 °C (Calduch *et al.* 2004).

Species fell into two groups with respect to pH optima. *Oidiodendron cerealis, O. chlamydosporicum, O. flavum, O. fuscum, O. griseum, O. maius, O. periconioides, O. rhodogenum, O. setiferum, O. tenuissimum, M. cancellatum,* and *M. arcticum* were acidophilic (pH optima <5) while *O. echinulatum, O. truncatum,* and *M. setosum* grew optimally at higher pH (>7).

Substrate degradation tests can distinguish among morphologically similar species. All species liquefied gelatin, and all but *O. truncatum* degraded potato starch. *Oidiodendron fuscum, M. cancellatum,* and *M. setosum* were unable to degrade cellulose azure. *Oidiodendron cerealis, O. periconioides, O. rhodogenum, O. setiferum, M. arcticum,* and *M. cancellatum* were unable to degrade TWEEN 20, while this ability varied within *O. chlamydosporicum*. Only *O. echinulatum* was unable to degrade pectin while this character was variable within *O. periconioides*. *Oidiodendron cerealis, O. flavum, O. fuscum, O. rhodogenum, O. tenuissimum, O. truncatum, M. cancellatum,* and *M. setosum* were unable to degrade tannic acid and *O. chlamydosporicum* and *M. arcticum* varied in this ability. Only *O. echinulatum* and *O. maius* var. *citrinum* consistently degraded lignin while isolates of *O. chlamydosporicum* varied in their ability to degrade this substrate (Table 4.1).

4.4. Keys to *Oidiodendron* species

Numbers in parentheses refer to the order in which the species descriptions are provided.

4.4.1. Synoptic Key to Oidiodendron *species*

Character	**Character State**	**Species**
Conidiomata	Present	*O. myxotrichoides* (18)
	Absent	All others
Melanized appendages	Simple, antler-like	*O. muniellense* (17) *O. setiferum* (22)
	Peridium-like	*O. hughesii* (14)
	Absent	All other
Chlamydospores	Present	*O. chlamydosporicum* (8)
	Absent	All others
"Geniculate conidiogenesis"	Present	*M. arcticum* (1)
	Absent	All others
Conidial colour	Darkly pigmented (melanized)	*M. striatosporum* (5) *O. cerealis* (7) *O. echinulatum* (9) *O. flavum* (11) *O. muniellense* (17) *O. myxotrichoides* (18) *O. periconioides* (19) *O. tenuissimum* (23) *O. truncatum* (24)
	Hyaline	*M. arcticum* (1) *M. cancellatum* (2) *M. emodense* (3) *M. setosum* (4) *O. ambiguum* (6) *O. chlamydosporicum* (8) *O. fuscum* (12) *O. griseum* (13) *O. maius* (15, 16)

		O. pilicola (20)
	Lightly pigmented	*O. fimicolum* (10) *O. hughesii* (14) *O. rhodogenum* (21) *O. setiferum* (22)
Conidial Ornamentation	Thickened ring	*O. cerealis* (7)
	Reticulate	*M. cancellatum* (2) *O. truncatum* (24)
	Warty or spiny	*O. ambiguum* (6) *O. echinulatum* (9) *O. periconioides* (19)
	Asperulate	*M. striatosporum* (5) *O. fimicolum* (10) *O. flavum* (11) *O. hughesii* (14) *O. muniellense* (17) *O. tenuissimum* (23)
	Indistinct	*M. arcticum* (1) *M. emodense* (3) *M. setosum* (4) *O. chlamydosporicum* (8) *O. fuscum* (12) *O. griseum* (13) *O. maius* (15, 16) *O. myxotrichoides* (18) *O. pilicola* (20) *O. rhodogenum* (21) *O. setiferum* (22)
Conidial Shape	Lens-shaped	*O. cerealis* (7)
	Globose to ellipsoidal	*O. ambiguum* (6) *O. echinulatum* (9) *O. fuscum* (12) *O. hughesii* (14)

		O. muniellense (17)
		O. myxotrichoides (18)
		O. periconioides (19)
	Barrel-shaped (truncate)	*M. cancellatum* (2)
		M. striatosporum (5)
		O. pilicola (20)
		O. truncatum (24)
	Ellipsoidal to elongate or cylindrical	*M. arcticum* (1)
		M. emodense (3)
		M. setosum (4)
		O. chlamydosporicum (8)
		O. griseum (13)
		O. maius (15, 16)
		O. rhodogenum (21)
		O. setiferum (22)
		O. tenuissimum (23)
	Variable	*O. fimicolum* (10)
		O. flavum (11)
Conidiophore Branching	Branched	*M. arcticum* (1)
		M. cancellatum (2)
		M. emodense (3)
		M. striatosporum (5)
		O. ambiguum (6)
		O. echinulatum (9)
		O. hughesii (14)
		O. muniellense (17)
		O. periconioides (19)
		O. pilicola (20)
		O. rhodogenum (21)
		O. setiferum (22)
		O. truncatum (24)
	Unbranched	*O. flavum* (11)
		O. fuscum (12)

		O. griseum (13) *O. maius* (15, 16) *O. tenuissimum* (23)
Conidiophore colour	Hyaline	*M. setosum* (4) *O. cerealis* (7)
	Variable	*O. chlamydosporicum* (8) *O. fimicolum* (10)
	Melanized	All others
Conidiophore texture	Highly asperulate	*O. fimicolum* (10)
	Smooth	All others
Colony colour	Yellow	*M. setosum* (4) *O. maius* var. *citrinum* (15)
	Off-white to gray	*M. arcticum* (1) *M. cancellatum* (2) *M. emodense* (3) *O. ambiguum* (6) *O. fimicolum* (10) *O. fuscum* (12) *O. griseum* (13) *O. maius* var. *maius* (16) *O. rhodogenum* (21)
	Pale brown	*O. echinulatum* (9) *O. flavum* (11)
	Dark brown/green	*M. striatosporum* (5) *O. cerealis* (7) *O. hughesii* (14) *O. muniellense* (17) *O. myxotrichoides* (18) *O. periconioides* (19) *O. setiferum* (22) *O. tenuissimum* (23) *O. truncatum* (24)
	Variable	*O. chlamydosporicum* (8)

Optimal Temperature	<20 °C	*M. cancellatum* (2)
		M. setosum (5)
		O. hughesii (14)
		O. myxotrichoides (18)
		O. truncatum (24)
	>20 °C	*O. chlamydosporicum* (8)
		O. muniellense (17)
		O. setiferum (22)
	20 °C	All others
Optimal pH	Basic (9-11)	*M. setosum* (4)
		O. echinulatum (9)
		O. truncatum (24)
	Acidic (3-5)	All others
Cellulose Degradation	No	*M. cancellatum* (2)
		M. setosum (4)
		O. fuscum (12)
	Yes	All others
Lignin (WDG) Degradation	Yes	*O. echinulatum* (9)
		O. maius var. *citrinum* (15)
	Variable	*O. chlamydosporicum* (8)
	No	All others
Lipid (TWEEN 20) Degradation	Yes	*M. setosum* (4)
		O. echinulatum (9)
		O. flavum (11)
		O. fuscum (12)
		O. maius (15, 16)
		O. tenuissimum (23)
		O. truncatum (24)
	No	*M. arcticum* (1)
		M. cancellatum (2)
		O. cerealis (7)
		O. griseum (13)
		O. periconioides (19)

		O. rhodogenum (21) *O. setiferum* (22)
	Variable	*O. chlamydosporicum* (8)
Pectin Degradation	No	*O. echinulatum* (9)
	Variable	*O. periconioides* (19)
	Yes	All others
Starch Degradation	No	*O. truncatum* (24)
	Yes	All others
Tannic Acid Degradation	Yes	*O. echinulatum* (9) *O. griseum* (13) *O. maius* (15, 16) *O. periconioides* (19) *O. setiferum* (22)
	No	*M. cancellatum* (2) *M. setosum* (4) *O. cerealis* (7) *O. flavum* (11) *O. fuscum* (12) *O. rhodogenum* (21) *O. tenuissimum* (23) *O. truncatum* (24)
	Variable	*M. arcticum* (1) *O. chlamydosporicum* (8)

4.4.2. Dichotomous Key to Oidiodendron *species*

1a. Conidia produced on fertile hyphae arising laterally or terminally from the melanized branches of a reticuloperidium-like conidioma............................*O. myxotrichoides* (18)

1b. Conidia produced on solitary conidiophores, conidiomata absent.................................2

2a. (1b) Conidiophores hyaline, typically <30 µm long (may be up to 130 µm long)...............3

2b. (1b) Conidiophores melanized, typically >5 µm long...4

3a. (2a) Colonies cream to yellow. Conidia hyaline, subglobose to elongate........*M. setosum* (4)

3b. (2a) Colonies dark brown to black. Conidia melanized, subglobose to lens-shaped with a thickened ring...*O. cerealis* (7)

4a. (2b) Conidiophores bearing melanized appendages at their apices................................5

4b. (2b) Conidiophores not bearing melanized appendages at their apices............................7

5a. (4a) Appendages highly branched and anastomosing to form a reticulate network, 60-300 µm diam. including peripheral spines. Conidia pale olive brown, produced *en masse* at the center of the reticulum..*O. hughesii* (14)

5b. (4a) Appendages scarcely branched to form 2-6 setiform hairs. Conidia pale brown, produced from fertile hyphae arising from the conidiophore apex or from appendage branching points or tips..6

6a. (5b) Appendages straight, up to 60 µm long. Conidia globose to subglobose, asperulate to echinulate..*O. muniellense* (17)

6b. (5b) Appendages often recurved, up to 130 µm long. Conidia subglobose to elongate or irregular, with smooth to faintly reticulate ornamentation........................*O. setiferum* (22)

7a. (4b) Fertile hyphae swollen to form chains of vesicles which form thick-walled, melanized, spiny, globose to ellipsoidal conidia..*O. periconioides* (19)

7b. (4b) Fertile hyphae not forming vesicles. Conidia thin- or thick-walled, hyaline or melanized, with indistinct, reticulate, asperulate, or warty ornamentation, subglobose to ellipsoidal, elongate, barrel-shaped or irregular..8

8a. (7b) Chlamydospores melanized, 3-6 x 2-4 µm, borne on repent hyphae and conidiophores. Conidiophores 5-70 µm long (mean < 20). Conidia hyaline, subglobose to elongate (1.5-3 x 1-2 µm)...*O. chlamydosporicum* (8)

8b. (7b) Chlamydospores absent. Conidiophores typically longer than 20 µm. Conidia hyaline or melanized, subglobose to ellipsoidal, elongate, barrel-shaped or irregular.....................9

9a. (8b) Conidiophores asperulate under light microscopy. Conidia hyaline to pale brown, elongate to barrel-shaped or irregular (3-6 x 2-3 µm)...............................*O. fimicolum* (10)

9b. (8b) Conidiophores smooth under light microscopy. Conidia hyaline or melanized, subglobose to ellipsoidal, elongate, barrel-shaped or irregular..................................10

10a. (9b) Conidia subglobose to barrel-shaped with truncate ends..................................11

10b. (9b) Conidia globose, ellipsoidal, subglobose, elongate or irregular, but neither barrel-shaped nor truncate...14

11a. (10a) Conidia melanized, produced either on conidiophores (<200 µm long) or directly from vegetative hyphae...12

11b. (10a) Conidia hyaline, produced on conidiophores (<150 µm long)...........................13

12a. (11a) Mature colonies olive-green with yellow margins. Conidia 2-7 x 1.5-2.5 µm, smooth to asperulate, produced on unbranched or branched conidiophores (<100 µm long) or directly from vegetative hyphae...*M. striatosporum* (5)

12b. (11a) Mature colonies brown to grey-green, yellow margin absent. Conidia 2-5 x 1-3.5 µm, with reticulate ornamentation, produced on branched conidiophores (20-200 µm long)..*O. truncatum* (24)

13a. (11b) Conidiophores dichotomously or trichotomously branched, 25-100 µm long. Conidia 1.5-3.5 x 1-2.5 µm, thick-walled with reticulate ornamentation............*M. cancellatum* (2)

13b. (11b) Conidiophores dichotomously branched, 100-150 µm long. Conidia 3-3.5 x 1.5-2 µm, thin-walled, smooth..*O. pilicola* (20)

14a. (10b) Conidia melanized..15

14b. (10b) Conidia hyaline...17

15a. (14a) Conidia globose to subglobose or broadly ellipsoidal, warty. pH optimum >7. Conidiophores dichotomously branched...*O. echinulatum* (9)

15b. (14a) Conidia subglobose to elongate or irregular with indistinct to asperulate ornamentation. pH optimum <7. Conidiophores unbranched.......................................16

16a. (15b) Colonies cream. Conidia subglobose to ellipsoidal, pyriform or irregular, thick-walled, smooth to asperulate. Conidiophores 25-80 µm long.....................*O. flavum* (11)

16b. (15b) Colonies brown. Conidia subglobose to elongate, with indistinct ornamentation. Conidiophores 30-250 µm long...*O. tenuissimum* (23)

17a. (14b) Colonies white to pale grey. Conidia produced in branching chains from fertile hyphae or in truncated chains (1-2 conidia) in whorls at the conidiophore apex. Conidia subglobose to elongate and irregular (1.5-3.5 x 1-2.5 µm). Conidiophores branched...*M. arcticum* (1)

17b. (14b) Colonies off-white, grey or yellow. Conidia produced only in branched chains from fertile hyphae. Conidia globose to ellipsoidal or subglobose to elongate. Conidiophores branched or unbranched...18

18a. (17b) Colonies off-white to grey or green-grey. Conidiophores branched. Conidia globose to ellipsoidal or subglobose to elongate and irregular..19

18b. (17b) Colonies off-white to grey or yellow. Conidiophores unbranched. Conidia subglobose to ellipsoidal or elongate..21

19a. (18a) Colonies off-white to grey, sometimes with diffusible red pigment. Conidiophores 30-85 µm long. Fertile hyphae dichotomously branched. Conidia subglobose to elongate or irregular, 1.5-5 x 1.5-2 µm with indistinct ornamentation.....................*O. rhodogenum* (21)

19b. (18a) Colonies grey or green-grey, red pigment absent. Conidiophores up to 200 µm long. Fertile hyphae often verticillate. Conidia globose to ellipsoidal or short cylindrical, 3-4.5 x 2.5 µm or 1.5-3.5 x 1.5-2 µm, smooth or verruculose..20

20a. (19b) Colonies grey. Conidiophores 100-200 µm long. Conidia globose to ellipsoidal, 3-4.5 x 2.5 µm, verruculose………………………………………………………*O. ambiguum* (6)

20b. (19b) Colonies grey or green-grey. Conidiophores 20->200 µm long. Conidia subglobose, ellipsoidal or short cylindrical, 1.5-3.5 x 1.5-2 µm, smooth…………………...*M. emodense* (3)

21a. (18b) Colonies off-white or yellow. Mean conidiophore length >100 µm. Conidia subglobose to elongate or cylindrical, produced in long undulating chains………………...22

21b. (18b) Colonies off-white to grey or grey-brown. Mean conidiophore length <100 µm. Conidia subglobose to elongate or cylindrical, produced in a dense head of non-undulating chains……………………………………………………………………………………..23

22a. (21a) Colonies yellow to yellow-green. Conidia yellow *en masse* with a rugose perispore. WDG +. Conidiophores 50-230 µm long………………………….*O. maius* var. *citrinum* (15)

22b. (21a) Colonies white to off-white. Conidia white *en masse* with an asperulate perispore. WDG-. Conidiophore 70-400 µm long……………………………..*O. maius* var. *maius* (16)

23a. (21b) Colonies off-white to grey. Conidiophores 25-130 µm long. Conidia subglobose to elongate or cylindrical, 1.5-5 x 1-2 µm with an asperulate perispore. Degrades cellulose and tannic acid but not lipids……………………………………………………...*O. griseum* (13)

23b. (21b) Colonies off-white to grey-brown. Conidiophores 15-40 µm long. Conidia subglobose to ellipsoidal, dimpled, 1.5-3 x 1-2 µm with an asperulate to verruculose perispore. Degrades lipid but not cellulose or tannic acid……………………..*O. fuscum* (12)

4.5. Species Descriptions

1. *Oidiodendron* anamorph of *Myxotrichum arcticum* Udagawa, Uchiyama & Kamiya, Mycotaxon 52: 198-204. 1994. **Figure 4.1.**

Colonies on CMA 23-25 mm diam at 28 days, white to pale grey, appressed; reverse dark brown. Conidiophores abundant, bearing masses of white conidia, smooth, melanized, dichotomously branched at apex, 20-(75)-215 x 2-4 µm. Conidiophores showing "geniculate conidiogenesis" and, thus, terminating in whorls of truncated chains of 1-2 conidia that are borne perpendicular to the conidiogenous cell, or otherwise terminating in hyaline, dichotomously branched fertile hyphae, 2-3 µm diam, that fragment to form chains of conidia. Conidia thin-walled, hyaline, subglobose to elongate and irregular, 1.5-(2.4)-3.5 x 1-(1.9)-2.5 µm, asperulate to spinulose under SEM. Maximal growth at 20 °C and pH 3. Degrades cellulose, gelatin, pectin, and starch; UAMH 7565 also degrades tannic acid.

Specimens Examined: **USA**, George Parks Hwy Road, Willow, north of Wasilla, Alaska, forest soil, 1992, Udagawa (UAMH 7565, *ex*-type); **Canada**, Mariana Lake, Alberta, decaying *Picea glauca* (Moench) Voss, 1997, Lumley (UAMH 9243).

Notes: The tall conidiophores and white conidia make this species superficially similar to *O. maius* var. *maius* but the conidia here are smaller and the chains of conidia are shorter and show less undulation. The peridial elements of the teleomorph are morphologically similar to those of sterile gymnothecia produced by *O. maius* var. *maius* (Rice & Currah 2002). *Oidiodendron fuscum, O. griseum*, and *M. emodense* have similar conidiophore lengths and dense conidiogenous heads. However, geniculate conidiogenesis is unique to *M. arcticum*. Molecular evidence suggests a close relationship between *M. arcticum* and *O. griseum* (Hambleton *et al.* 1998).

2. *Oidiodendron* anamorph of *Myxotrichum cancellatum* Phillips, Grevillea 13: 51-52. 1884. **Figure 4.2**.

Colonies on CMA 11-13 mm diam at 28 days, white to grey, appressed at margins; reverse purple to black. Conidiophores and aerial hyphae abundant. Conidiophores bearing masses of off-white to grey conidia, melanized, smooth, branched dichotomously or trichotomously at apex, 25-(50)-100 x 2-4 µm. Conidia thick-walled, hyaline to lightly melanized at maturity, subglobose to barrel-shaped, reticulately ornamented with a rugose perispore, 1.5-(2.6)-3.5 x 1-(1.7)-2.5 µm; connectives visible between adjacent conidia. Maximal growth at 15-20 °C and pH 5. Degrades gelatin, pectin, and starch.
Specimen Examined: **Japan**, Tokyo, soil, 1959, Udagawa (UAMH 1996).

Notes: Dalpé (1991) noted that this species uses Czapek cellulose agar but in this study the cellulose azure test was negative. *Oidiodendron truncatum* is similar but differs in having melanized conidia and dichotomously branched conidiophores.

3. *Oidiodendron* anamorph of *Myxotrichum emodense* Udagawa & Uchiyama, Mycoscience 40: 292-296. 1999. **Figure 4.3**.

Colonies on oat agar (OA) 28-30 mm diam at 28 days at 25 °C, thin, with submerged vegetative mycelium, appearing granular due to the production of abundant ascomata intermixed with aerial hyphae and conidial heads; at first grayish yellow, becoming greenish gray or olivaceous black, with clear exudate; reverse dull green or grey olivaceous; conidiogenesis moderate. Colonies on potato carrot agar (PCA) 21-22 mm diam at 28 days at 25 °C, floccose, plane, with thin vegetative mycelium, producing abundant conidia, greenish grey or smoke gray; exudate absent; reverse uncoloured to brownish grey or smoke grey. Conidiophores erect, arising from vegetative mycelium or aerial hyphae, straight below, branching at the top to produce an arborescent, olivaceous brown head; conidiophores olivaceous brown to dark brown, 25->200 µm long x 1.5-2.5 µm diam, straight, septate, thick-walled, smooth or sometimes with black nodes; branches hyaline to pale olivaceous brown, 10-60 x 2-2.5 µm, smooth-walled, repeatedly rebranched, frequently forming a verticillate whorl of 4-6 narrow fertile hyphae. Fertile hyphae hyaline, cylindrical, 1.2-1.5 µm diam, fragmenting to form conidial chains. Conidia hyaline, pale grayish green *en masse*, subglobose, ovoid, ellipsoidal, or short cylindrical, 1.5-3.5 x 1.5-2 µm, almost smooth-walled, truncate at one or both ends, connectives sometimes visible between conidia. Weakly cellulolytic. Reduced growth at 15 °C. Habitat: grassland soil, Nepal. Description from Udagawa & Uchiyama (1999).

Notes: This species is morphologically similar to *O. fuscum*, *O. griseum*, and *M. arcticum* but *M. arcticum* has geniculate conidiogenesis and *O. griseum* and *O. fuscum* have unbranched conidiophores and dichotomously branched fertile hyphae that are distinct from the branched conidiophores and verticilloid whorls formed in *M. emodense*.

4. *Oidiodendron* anamorph of *Myxotrichum setosum* (Eidam) Orr & Plunkett, Can J Bot 41: 1470-1471. 1963. **Figure 4.4**.

Colonies on CMA 14-15 mm diam at 28 days, cream to pale yellow, appressed at margins; reverse cream to orange. Aerial conidia abundant, off-white to yellow *en masse*. Conidiophores typically less than 5 µm long or absent, hyaline to lightly melanized. Longer, hyaline conidiophores (30-140 µm) were observed by Sigler and Carmichael (1976). Conidia hyaline, subglobose to elongate or irregular, 2-(3.6)-5 x 1.5-(2)-3 µm, produced in dichotomously branched chains at the apices of short conidiophores or directly from vegetative hyphae. Maximal growth at 15 °C and at alkaline pH. Degrades gelatin, pectin, lipid, and starch. Specimens Examined: **Canada**, Mt. Allen, Kananaskis, Alberta, soil, 1971, Bissett (UAMH 3835); washed mineral soil particle, 1971, Bissett (UAMH 4535).

Notes: The absence of melanized conidiophores is unusual in species of *Oidiodendron*. This character, along with the yellow colour of the colony, readily distinguishes the anamorph of *M. setosum* from other species. Molecular evidence supports a presumed relationship with other species of *Oidiodendron* (Hambleton *et al.* 1998). *Oidiodendron sulphureum* (Stalpers 1974), if distinct from *O. flavum* or encountered again, would be similar to the anamorph of *M. setosum* but could be distinguished based on its darker yellow colonies, the presence of some melanized conidiophores, and curved fertile hyphae. More details about *O. sulphureum* are found under *O. flavum*.

5. *Oidiodendron* anamorph of *Myxotrichum striatosporum* (Barron & Booth) Sigler, Mycotaxon 4: 385-388. 1976. **Figure 4.5**.

≡*Arachniotus striatosporus* Barron & Booth *fide* von Arx
≡*Byssoascus striatisporus* (Barron & Booth) von Arx *fide* Sigler & Currah

Colonies 15-20 mm diam at 14 days at 25 °C on potato dextrose agar (PDA) and malt extract agar (MEA); 10 mm diam at 14 days and 25 °C on Czapek's synthetic agar. Colonies bright yellow at first, becoming dark olivaceous in the center, smooth to slightly floccose, becoming funiculose; when mature olive-green with yellow margins, weakly zonate, with edges slightly irregular to scalloped. A thick turf of conidia is eventually produced which may crack irregularly in older cultures. Colony description from Barron & Booth (1966). Conidiophores present or absent, lower one fifth to one third [12-(35)-62.5 x 2-3 μm] melanized, unbranched or dichotomously branched; upper portion (up to 50 μm long) hyaline to subhyaline, branched dichotomously to produce fertile hyphae, 1-1.5 μm diam, that fragment to form long, branched chains of conidia. Conidia barrel-shaped, smooth to asperulate, truncate with pigmented basal scars, hyaline to yellow when immature, yellow-brown to brown at maturity, 2-(4)-7 x 1.5-(2)-2.5 μm.

Specimen Examined: **Canada**, Bradford Marsh, Ontario, soil, 1960, Barron (UAMH 3758, *ex-type Arachniotus striatosporus*). Degenerate and no longer producing conidia. A permanent slide of this specimen was obtained from UAMH and used to obtain microscopic measurement and descriptions.

Notes: This species is known only from the type but it is easily distinguished from other species of *Oidiodendron* based on its olive green colonies that have yellow margins and by its yellow to brown, truncate, asperulate conidia.

6. *Oidiodendron ambiguum* (Peyronel) Malan, Nuovo Giornale Botanico Italiano 56: 753-737. 1949. **Figure 4.6.**

≡*Dicyma ambigua* Peyronel *fide* Malan (1949)

Colonies "large" (quote from original description, dimensions unspecified), round, initially ash grey, later darkening to an intermediate mouse grey. Vegetative hyphae septate, mostly hyaline, 1-2.5 µm diam, some darker, 3-7 µm diam. Conidiophores arising from dark sections of the hyphae interspersed at relatively regular intervals among the hyaline mycelium, erect, rigid, septate, melanized at maturity, 100-250 x 2-4 µm, with apices bearing dichotomous primary branches with many dichotomous, verticillate or sympodial subbranches. Conidia formed in branched chains along swollen terminal branches, hyaline, globose to ellipsoidal, minutely verruculose, 3-4.5 x 2.5 µm, grey *en masse*, giving the colony its characteristic colour. Habit: air samples, alpine forest. Description from Peyronel (1914) and Malan (1949), translated from Italian. [UAMH 8443 (=ATCC 36256) from Italy, soil of snow valley, Mosca (from ATCC as *O. ambiguum*) was reidentified as *O. truncatum*].

Notes: Peyronel (1914) was uncertain about the mode of conidial development and, as a result, his description and figures are unclear. Malan (1949) considered it arthroconidial, placed it within *Oidiodendron*, and provided clearer illustrations but added little to the written description. The illustrations provided by Malan (1949), coupled with its habitat data and the assertion that it is the anamorph of *Myxotrichum aeruginosum*, suggest that it is likely an *Oidiodendron* species but neither Peyronel nor Malan specified a type or deposited specimens. The only record of *O. ambiguum* since Malan is ATCC 36256 (=UAMH 8443), which I reidentified as *O. truncatum* on the basis of its dark, barrel-shaped conidia with reticulate ornamentation. If encountered again, *O. ambiguum* would be distinguished by its verruculose, hyaline, globose to ellipsoidal conidia.

7. *Oidiodendron cerealis* (Thümen) Barron, Can J Bot 40: 594-595. 1962. **Figure 4.7.**

≡*Trichosporium cerealis* Thümen *fide* Barron (1962)
≡*Stephanosporium cereale* (Thümen) Swart *fide* Domsch *et al.* (1980)
= *Oidiodendron nigrum* Robak *fide* Barron (1962)

Colonies on CMA 30-34 mm diam at 28 days, green-grey (CBS 349.62) or pale with clumps of brown to black conidia (UAMH 504, 1522); reverse green-grey to black (CBS 349.62) or dark brown to black beneath areas of heavy sporulation (UAMH 504, 1522). Aerial hyphae abundant and hyaline in UAMH 504 and 1522 but scarce in CBS 349.62. Conidiophores short, branched, hyaline to lightly melanized, 5-(15)-28 x 2-3 µm. Conidia melanized, in short chains or appearing clumped at conidiophore apex, subglobose to lens-shaped with a thickened ring and highly rugose (wrinkled) perispore, 2.5-(3.3)-4 x 2-(2.8)-4 µm. Maximal growth at pH 3-5 and 20 °C. Degrades cellulose, gelatin, pectin, and starch.

Specimens Examined: **Italy**, Piedmont, alpine meadow soil, 1962, Dal Vesco (CBS 349.62); **Canada**, Edmonton, Alberta, human hair, 1956, Carmichael (UAMH 504); Bradford Marsh, Ontario, peat soil, 1960, Barron (UAMH 1522).

Notes: This species is unique because of its hyaline conidiophores and lens-shaped arthroconidia with thickened rings of cell wall material. These features led to its placement outside of the genus *Oidiodendron*. However, molecular analyses support its placement within *Oidiodendron* (Hambleton *et al.* 1998) and its morphological dissimilarity is significant only at the species level.

8. *Oidiodendron chlamydosporicum* Morrall, Can J Bot 46: 205-206. 1968. **Figure 4.8.**
= *Oidiodendron scytaloides* Gams & Söderström

Colonies on CMA 9-16 mm diam at 28 days, cream or pale grey to green grey or brown, darker at margins, appressed; reverse cream to dark brown at center. Conidia and chlamydospores pale to brown *en masse*, produced on repent hyphae at the surface of the agar or on conidiophores present at the center of the colonies. Conidiophores (2-3.5 µm diam) ranging from short, branched, lightly pigmented to melanized, 3-(10)-17 µm long to erect and melanized, 5-(35)-70 µm, bearing chains of hyaline conidia interspersed with melanized chlamydospores. Conidia thin-walled, hyaline, globose to subglobose or elongate, 1.5-(2.5)-5 x 1-(1.7)-2.5 µm, produced in chains arising from vegetative hyphae or from conidiophores. Chlamydospores subglobose to barrel-shaped or pyriform, thick-walled, melanized, 3-(4)-7 x 2-(3.5)-4 µm, abundant, arising singly or in short chains from vegetative hyphae or conidiophores. Under SEM, conidia minutely asperulate, chlamydospores pitted. Maximal growth at 20-25 °C and pH 3. Degrades cellulose, gelatin, pectin, starch; UAMH 6520, 8510, and 9751 degrade lipid; UAMH 6520 and 6521 degrade lignin; UAMH 9751 degrades tannic acid.

Specimens Examined: **Canada**, Candle Lake, Saskatchewan, boreal forest soil, 1964, Morrall (UAMH 6520, *ex*-type); Perryvale, Alberta, *Sphagnum fuscum* (Schimp.) Klinggr., bog, Thormann (UAMH 9749, as *O. scytaloides*); **Sweden**, humus, *Picea abies* (L.) Karst. forest, 1973, Söderström & Bååth (UAMH 6521, *ex*-type *O. scytaloides*); Kongalund, illuvial soil, *Picea abies* forest, 1973, Söderström & Bååth (UAMH 6527, as *O. scytaloides*); **Germany**, Freiberg, roots of dying *Abies alba* Miller, 1981, Schuler (UAMH 8510, as *O. scytaloides*).

Notes: *Oidiodendron chlamydosporicum* was described as having subglobose to globose, terminal or intercalary chlamydospores, 4-9 µm diam, and subglobose to ellipsoidal or cylindrical conidia, 2-6 x 1.2-2 µm (Morrall 1968). *Oidiodendron scytaloides* was described with smaller (3-5 x 2.5-3 µm), ellipsoidal chlamydospores formed in short, terminal, lateral, or intercalary chains and shorter (2-4 x 1-2 µm), cylindrical or ellipsoidal conidia (Gams & Söderström 1983). However, *ex*-type cultures of the two species are indistinguishable in terms of chlamydospore shape and size, with the shape ranging from subglobose to barrel-shaped or pyriform and the size ranging from 3-7 x 2-4 µm in each isolate. Moreover, conidial size and shape, which overlapped in the original descriptions, ranges from 1.5-5 x 1-2.5 in all isolates. *Oidiodendron chlamydosporicum* has priority over *O. scytaloides*, which is here relegated to synonymy. Molecular analyses support their conspecificity (Hambleton *et al.* 1998, Calduch *et al.* 2004).

9. *Oidiodendron echinulatum* Barron, Can J Bot 40: 595-597. 1962. **Figure 4.9**.

Colonies on CMA 35-37 mm diam at 28 days, off-white to tan, floccose, with brown exudate; reverse dark brown. Aerial hyphae hyaline, abundant. Conidiophores abundant, bearing masses of brown conidia, dichotomously branched, melanized, smooth, 12-(35)-88 x 2-5 µm. Fertile hyphae hyaline, 2-3 µm diam, dichotomously branched, fragmenting into chains of conidia. Conidia thick-walled, melanized, subglobose or ellipsoidal, warted at maturity, produced at apices of conidiophores or in chains branching directly from vegetative hyphae, 2-(3)-4 x 2-(2.6)-3 µm. Growth suppressed by daylight. Maximal growth at pH 11 and 20 °C. Degrades cellulose, gelatin, lipid, starch, tannic acid, and lignin.

Specimen Examined: **Canada**, Ontario, peat soil, cedar bog, Barron (UAMH 8467, authentic).

Notes: *Oidiodendron echinulatum* can be distinguished from others in the genus by its branched conidiophores, warted conidia, growth suppression by light, maximal growth at pH 11, and positive WDG reaction. *Oidiodendron periconioides* is similar but has spiny, globose conidia, is WDG negative, grows optimally at acidic pH, and shows no inhibition by light.

10. *Oidiodendron fimicolum* Rice & Currah, in press 1. **Figure 4.10**.

= *Oidiodendron sindenia* nomen nudum *fide* Rice & Currah (in press 1)

Colonies on CMA 19-26 mm diam at 28 days, off-white to beige or pale grey, appressed with concentric rings of abundant conidiophores bearing masses of off-white to beige conidia; reverse olivaceous. Conidiophores present or absent, branched or unbranched, melanized, asperulate to scaly, 20-(50)-100 x 2-4 µm. Fertile hyphae hyaline, 2 µm diam, fragmenting to form short, dichotomously branched chains of arthroconidia. Conidia thick-walled, hyaline to light brown, barrel-shaped to elongate or irregular, more or less truncate at one or both ends, asperulate, 3-(4.9)-6 x 2-(2.4)-3 µm.

Specimens Examined: **USA**, St. Louis, Missouri, mushroom compost, 1976, Beyer [UAMH 10459 (=DC 60), *ex*-type]; California, mushroom compost, 1976, Beyer [UAMH 10523 (=DC 61)].

Notes: D. M. Beyer labeled material he sent for deposit in ATCC in 1976 "*O. sindenia* Beyer", but never validly published the name. The material deposited at ATCC was listed in the catalogue under *O. sindenia* but it has since died (ATCC, pers. comm.). In 2002, Beyer sent me the cultures from the Pennsylvania State Mushroom Spawn Laboratory. One of these, DC 60 (=UAMH 10459), is reportedly from the same collection as the material deposited in ATCC. *Oidiodendron fimicolum* is the only *Oidiodendron* species that has consistently asperulate conidiophores, a character that, coupled with conidial ornamentation under SEM, distinguishes it from the morphologically similar *O. flavum*.

11. *Oidiodendron flavum* von Szilvinyi, Zbl Bakt Abt II, 103: 179. 1941. **Figure 4.11**.

Colonies on CMA 27-28 mm diam at 28 days, cream to yellow-brown, appressed; reverse dark brown. Hyphae submerged at colony margins. Conidiophores abundant, bearing masses of brown to grey conidia, smooth, unbranched, melanized, 25-(40)-80 x 2-4 µm. Fertile hyphae hyaline, 2-3 µm diam, 2-4 times dichotomously branched, fragmenting into short chains of 2-10 conidia. Conidia thin-walled, hyaline and elongate when immature, becoming globose to irregular, barrel-shaped, ellipsoidal or pyriform, thick-walled, melanized, smooth to asperulate or dimpled, 2.5-(3.3)-4 x 2-(2.8)-3 µm at maturity. Maximal growth at pH 3 and 20 °C. Degrades cellulose, gelatin, lipid, pectin, and starch.

Specimen Examined: **Canada**, Aberfoyle, Ontario, peat soil, cedar bog, Barron (UAMH 1524, authentic).

Notes: *Oidiodendron flavum* is distinguished by the wide variation in the shape of mature melanized conidia and by the changes in the shape and pigmentation of the conidia during maturation. *Oidiodendron fimicolum* is similar because it also displays a range of conidial shapes and pigmentation, but *O. flavum* differs in having smooth conidiophores and relatively round and smooth conidia. Molecular evidence suggests a close relationship between *O. flavum* and *O. griseum* (Hambleton *et al.* 1998, Lacourt *et al.* 2001, Sigler & Gibas, in press). However, the consistency of the phenotypic differences between authentic strains of the two species merits maintenance of the two names. Stalpers (1974) transferred *Oedocephalum sulphureum* to *Oidiodendron* as *Oidiodendron sulphureum* and suggested that it was similar or identical to *O. flavum* because the conidial dimensions reported by Stalpers (3.8-5 x 2.5-3.3 µm) are similar to those given by von Szilvinyi (1941) (3.4-5.7 x 2.5-3.4 µm) and because the curved branches on the fertile hyphae were also mentioned by Barron (1962). The brief description provided by Stalpers (1974) does not provide measurements for conidiophore length, reporting them as "rather short or absent, to 3.5 µm wide, with a pigmented, sometimes roughened basal part and a hyaline, repeatedly branched upper part" and the conidiophore is not shown in his illustration. No cultures are available and I have not examined the type, so I am unable to ascertain the precise placement of this species from Stalpers' description and illustrations and I am including it under *O. flavum*. If encountered again, *O. sulphureum* could be distinguished by its reportedly short conidiophores, sulphur-yellow colonies, and curved fertile hyphae.

12. *Oidiodendron fuscum* Robak, Saertryk av Nyt Mag Naturvidensk 71: 249-251. 1932. **Figure 4.12**.

Colonies on CMA 24-26 mm diam at 28 days, off-white to pale grey, appressed; reverse grey-brown to black. Conidiophores abundant, bearing masses of off-white to grey conidia, smooth, unbranched, melanized, 15-(25)-40 x 2-3 µm. Fertile hyphae hyaline, dichotomously branched, fragmenting to form chains of conidia in a dense head. Conidia thin-walled, hyaline to lightly pigmented, dimpled, subglobose to ellipsoidal with an asperulate to minutely verruculose perispore, 1.5-(2)-3 x 1-(1.5)-2 µm. Maximal growth at pH 3 and 20 °C. Degrades gelatin, lipid, pectin, and starch.

Specimen Examined: **Norway**, wood pulp, Robak (UAMH 8511, *ex*-type).

Notes: Robak (1932) described *O. fuscum* as having grey-brown to brown colonies, featuring smooth, branched or unbranched conidiophores 60-265 µm long, averaging 110-120 µm, as well as hyaline to greenish-brown conidia 1.6-3.6 x 1.2-2.2 µm, averaging 2.4 x 1.7 µm. Barron (1962) made *O. fuscum* a synonym of *O. tenuissimum* and described *O. tenuissimum* as a variable species with off-white to grey or brown colonies and hyaline to pigmented conidia. Nuclear ribosomal DNA sequence analyses (Hambleton *et al.* 1998) indicated that *O. tenuissimum sensu* Barron comprises two distinct lineages. The first, containing UAMH 8511, was designated "*O. tenuissimum*" and the other lineage was called "*O.* sp. nov." (Hambleton *et al.* 1998). However, SEM examination of the conidia of UAMH 8511, 8513 ("*O.* sp. nov."), and the type specimen of *Periconia tenuissima* showed that UAMH 8511 was distinct, while UAMH 8513 looked the same as the type of *P. tenuissima*. UAMH 8511 also differs in cultural morphology from the type of *P. tenuissima* (Hambleton, pers. comm.). I have restored *O. fuscum* as a distinct species on the basis of these morphological and molecular differences and suggest its reinstatement as the type of the genus. Recent sequence data (Sigler & Gibas, in press) indicate that the situation may be more complex with additional lineages included in *O. tenuissimum sensu* Barron.

Oidiodendron fuscum is morphologically similar to *O. griseum, O. maius* var. *maius*, and the anamorphs of *M. arcticum* and *M. emodense*. On average, it has shorter conidiophores than these other species and the conidia are shorter than in *O. griseum* and *O. maius* var. *maius*. It lacks the geniculate conidiogenesis of *M. arcticum* and the verticillate fertile hyphae of *M. emodense*. Morphological differences between the conidia of *O. fuscum* and *O. griseum* are best observed using SEM. *Oidiodendron fuscum* produces subglobose to ellipsoidal, dimpled, minutely verruculose conidia while *O. griseum* has subglobose to cylindrical, asperulate conidia.

13. *Oidiodendron griseum* Robak, Saertryk ur Svensk Skogvårdsföreningens Tiskr 3-4: 440. **Figure 4.13**.

Colonies on CMA 26-32 mm diam at 28 days, off-white to pale grey, appressed; reverse dark green-grey to black. Conidiophores abundant, bearing masses of off-white to grey conidia, smooth, unbranched, melanized, 25-(60)-130 x 2-5 µm. Fertile hyphae hyaline, 2-3 µm diam, dichotomously branched with acute branch angles, fragmenting to form long chains of up to 30 conidia in a dense fertile head. Conidia thin-walled, hyaline, subglobose to elongate or cylindrical, 1.5-(2.5)-5 x 1-(1.5)-2 µm with an asperulate perispore. Maximal growth at pH 3 and 20 °C. Degrades cellulose, gelatin, pectin, starch, and tannic acid.

Specimens Examined: **Sweden**, wood pulp, 1960, Melin (UAMH 1403, authentic); **Canada**, Westlock, Alberta, wood chips and bark, *ex* logging truck, Sigler (UAMH 4080); Slave Lake, Alberta, roots of *Vaccinium myrtilloides* Michx., *Pinus banksiana* Lamb. stand, sand dune, Hambleton (UAMH 8925).

Notes: *Oidiodendron griseum* is morphologically similar to *O. maius* var. *maius*, *O. fuscum*, and the anamorphs of *M. arcticum* and *M. emodense*. It lacks the geniculate conidiogenesis of *M. arcticum* and has unbranched conidiophores and dichotomously branched fertile hyphae as opposed to the branched conidiophores and verticillate fertile hyphae of *M. emodense*. Historically, there have been problems distinguishing isolates of *O. griseum* with longer than average conidiophores from isolates of *O. maius* var. *maius* (Hambleton & Currah 1997, Hambleton *et al.* 1998). However, the fertile hyphae of *O. griseum* have narrower branch angles and are less undulate than those of *O. maius* var. *maius*. The average conidiophore length in *O. griseum*, <100 µm, is less than in *O. maius* var. *maius*, >100 µm. Conidia of *O. griseum* are shorter on average (<3 µm) than those of *O. maius* var. *maius* (>3 µm).

Molecular studies have indicated a complex relationship between *O. griseum* and the polyphyletic *O. tenuissimum sensu* Barron (Hambleton *et al.* 1998, Lacourt *et al.* 2001, Hambleton, unpublished). Hambleton *et al.* (1998) found that isolates of *O. griseum* and *O. tenuissimum* produced indistinguishable restriction fragment length polymorphism (RFLP) patterns but formed distinct clusters based on ITS sequence data. A similar study (Lacourt *et al.* 2001), using a different set of isolates did not separate the two species using ITS sequence data. Hambleton (unpublished) has found that a clade that included all sequenced isolates identified as *O. griseum* and *O. tenuissimum sensu* Barron is so broad that it encompasses isolates of all the other sequenced *Oidiodendron* species. However, with the division of *O. tenuissimum sensu* Barron into *O. fuscum* and *O. tenuissimum sensu stricto*, *O. griseum* and *O. tenuissimum* are morphologically and physiologically distinct.

Oidiodendron griseum is morphologically most similar to *O. fuscum*. According to Robak's original descriptions of *O. griseum* (Melin & Nannfeldt 1934) and *O. fuscum* (Robak 1932), the two differ primarily in colony morphology and show only slight differences in conidiophore lengths and conidial dimensions. Robak described the colonies of *O. griseum* as green-grey with a dark green-black reverse (Melin & Nannfeldt 1934) and the colonies of *O. fuscum* as brown or grey-brown with a brown-black reverse (Robak 1932). I did not observe these cultural differences, possibly because different growth media were used. Both *O. griseum* and *O. fuscum* were similar in having off-white to grey colonies with a dark grey to black reverse.

Furthermore, conidiophore lengths and conidial dimensions given for the two species overlap. In *O. griseum*, the conidiophores range in length from 40-150 µm, averaging 90-100 (Melin & Nannfeldt 1934), while those of *O. fuscum* range from 60-265 µm, averaging 110-120 µm (Robak 1932). Conidia of *O. griseum* are 2-3.6 x 1.6-2 µm, averaging 2.6x1.8 µm (Melin & Nannfeldt 1934), while those of *O. fuscum* are 1.6-3.6 x 1.2-2.2 µm, averaging 2.4 x 1.7 µm (Robak 1932). I observed a narrower range in conidiophore lengths (25-130 µm) than that reported by Robak (Melin & Nannfeldt 1934), although there is considerable overlap. My measurement of mean conidiophore length (60 µm) is smaller than that reported by Robak (Melin & Nannfeldt 1934). These differences may be explained by my use of slide cultures and different media. I observed a wider range of conidial lengths (1.5-5 µm) but mean dimensions (2.5 x 1.5 µm) were similar to Robak's (Melin & Nannfeldt 1934). My measurements for *O. griseum* fall between the measurements I obtained for *O. fuscum* and those given in the original description (Robak 1932).

In general, my isolates of *O. griseum* have longer conidiophores (25-130 µm) than the *ex*-type of *O. fuscum* (15-40 µm). Conidia of *O. griseum* also differ from those of *O. fuscum* under SEM. My isolates of *O. griseum* have relatively long (1.5-5 µm), cylindrical conidia with an asperulate perispore while *O. fuscum* has relatively short (1.5-3 µm), subglobose to ellipsoidal conidia with an asperulate to minutely verruculose perispore. My isolates of *O. griseum* degrade cellulose and tannic acid and are unable to degrade lipid (TWEEN 20), while *O. fuscum* able to degrade lipid but not cellulose and tannic acid. Additional cultural and molecular differences between *O. fuscum* and *O. griseum* (Sigler & Gibas, in press) support recognizing them as distinct.

14. *Oidiodendron hughesii* Udagawa & Uchiyama, Can J Bot 76: 1641-1643. **Figure 4.14.**
= *Oidiodendron reticulatum* Calduch, Stchigel, Gené & Guarro

Colonies on PCA 12-13 mm diam at 21 days at 15 °C, 3-4 mm diam at 21 days at 25 °C, green-grey, becoming dark green to olivaceous black with age, appressed; reverse uncoloured to brown-grey; exudate absent. Conidia abundant after 14 days. Colonies on OA growing more slowly than on PCA, bearing conidiophores in dense stands; reverse red-brown. Conidiophores erect, 60-100 x 2.5-3 µm, melanized, unbranched and smooth walled below and asperulate and darkened above, branched and anastomosed to form a globose reticulum (60-160 µm diam; 250-280 µm diam when peripheral spines are included). Peripheral spines appendage-like, septate, dark olive brown, basally asperulate, with 1-2 branchlets arising near base; apices pointed, lighter in colour, and smoother than the basal region. Fertile hyphae 1.5-2.5 µm diam, arising from lateral branches of reticulum elements, verticillate, hyaline, smooth-walled, fragmenting to produce conidia. Conidia hyaline to pale olive-brown *en masse*, oval to ellipsoidal, thick-walled, asperulate, 2-4 x 1.5-2.5 µm. Simple conidiophores also produced, melanized, smooth, branched at apex to produce a dense head of fertile hyphae. Optimal growth at 15 °C. Habitat: forest soil. Description from Udagawa & Uchiyama (1998).

Notes: Calduch *et al.* (2004) distinguish *O. reticulatum* from *O. hughesii* on the basis of appendage ornamentation, conidial colour, and temperature optima. In *O. reticulatum*, the appendages are verruculose along their entire length while in *O. hughesii* they are smooth at their apices. The conidia of *O. reticulatum* are described as pale brown to olivaceous (Calduch *et al.* 2004) while those of *O. hughesii* are described as hyaline to pale olive brown *en masse* (Udagawa & Uchiyama 1998). These differences are slight in light of the similarities between the two species in colony morphology, reticulum dimensions, and conidial size, shape, and ornamentation (Udagawa & Uchiyama 1998, Calduch *et al.* 2004). These minor differences become less credible considering that only one isolate of each was described. Differences in appendage ornamentation and conidial pigmentation could reflect either intraspecific variation among isolates or differences in developmental stage. Calduch *et al.* (2004) report that *O. reticulatum* grows optimally at 25 °C while *O. hughesii* grows optimally at 15 °C. However, they also note that, on some media, growth of *O. reticulatum* is similar at 15 and 25 °C (Calduch *et al.* 2004). It is plausible that this physiological difference has been overstated and is due to ecological rather than phylogenetic differences. Udagawa and Uchiyama (1998) isolated *O. hughesii* from a cool, temperate, alpine site while Calduch *et al.* (2004) isolated *O. reticulatum* from a warm, subtropical site in Spain. The differences between *O. hughesii* and *O. reticulatum* are not significant at the species level and suggest that they are synonymous. There are no sequence data for *O. hughesii*.

15. *Oidiodendron maius* Barron var. *citrinum* Rice & Currah, comb. nov. **Figure 4.15.**
≡*Oidiodendron citrinum* Barron, Can J Bot 40: 597. 1962 (Basionym)

Colonies on CMA 30-36 mm diam at 28 days, yellow to yellow-green, appressed; reverse pale brown to dark brown in the center. Conidiophores abundant, bearing masses of yellow conidia, tall, unbranched, melanized, smooth, 50-(120)-230 x 2-4 µm. Fertile hyphae hyaline, 2-3 µm diam, dichotomously branched, fragmenting to form long undulating chains of conidia. Conidia thin-walled, hyaline, subglobose to elongate, 1.5-(2.8)-5 x 1-(1.8)-2.5, with a rugose perispore. Maximal growth at pH 3-5 and 20 °C. Degrades cellulose, gelatin, lipid, pectin, starch, tannic acid, and lignin.

Specimens Examined: **Canada**, Guelph, Ontario, soil, cedar bog, Barron (UAMH 1525, *ex*-type *O. citrinum*); Six Mile Lake, Muskoka District, Ontario, *ex* black sclerotia in stream drift, March 1991, Malloch (UAMH 7089); Slave Lake, Alberta, *ex* black mycorrhizal root tip (*Cenococcum* Moug. & Fr.) of *Arctostaphylos uva-ursi* (L.) Spreng., *Pinus banksiana* stand on sand dune, 1998, Hambleton (UAMH 9275).

Notes: *Oidiodendron citrinum* is sufficiently similar to *O. maius* that it can be considered a subspecific taxon within *O. maius*, which was described in the same publication (Barron 1962). Because *O. maius* is much more common in the literature, it is given priority. These two facies are recognized at the varietal level, rather than as a subspecies, because the latter term implies the existence of intermediate forms and differences in distribution (Hawksworth 1974). There are few data concerning the distribution and/or possible intergradation of these taxa that would support designating them as subspecies.

The conidiophores and conidia are similar to *O. maius* var. *maius* but the two can be distinguished on the basis of colony colour, conidial ornamentation under SEM, and WDG reaction. *Oidiodendron maius* var. *citrinum* has yellow colonies, conidia with a rugose perispore, and a positive WDG reaction while *O. maius* var. *maius* has white colonies, conidia with an asperulate perispore, and a negative WDG reaction. Molecular analyses indicate that these differences are probably not significant at the species level leading to suggestions that *O. maius* and *O. citrinum* are conspecific or that *O. citrinum* is a subspecies of *O. maius* (Hambleton *et al.* 1998, Lacourt *et al.* 2001, Sigler & Gibas, in press). Additional physiological (Rice & Currah, in press 1) and morphological (Sigler & Gibas, in press) characters support a close relationship between these taxa.

16. *Oidiodendron maius* Barron var. *maius*. Can J Bot 40: 600-602. 1962. **Figure 4.16**.

Colonies on CMA 29-38 mm diam at 28 days, white to off-white or grey, appressed; reverse pale grey to dark brown in center. Conidiophores abundant, tall, dark, bearing masses of three conidia, unbranched, smooth, 70-(185)-390 x 2-4 µm. Fertile hyphae hyaline, 2-3 µm diam, dichotomously branched, fragmenting into long, undulating, chains of conidia. Conidia thin-walled, hyaline, subglobose to elongate, 2-(3.3)-5 x 1-(1.7)-2.5 µm, with an asperulate perispore.

Maximal growth at pH 3 and 20 °C. Degrades cellulose, gelatin, lipid, pectin, starch, and tannic acid.

Specimens Examined: **Canada**, Ontario, soil, cedar bog, Barron (UAMH 1540, *ex*-type); Alberta, roots *Oxycoccus quadripetalus* Gilib, *Picea mariana* Miller bog, Hambleton (UAMH 8920); Perryvale, Alberta, decomposing *Sphagnum fuscum*, bog, Thormann (UAMH 9749); Fort McKay, Alberta, roots *Vaccinium myrtilloides*, disturbed sand hill, Hill-Rackette (UAMH 10460); Finland, Kevo, Research Station, roots *Vaccinium vitis-idaea* L., *Betula* L.-dominated fjell, Currah (UAMH 10461).

Notes: *Oidiodendron maius* var. *maius* is the only species in the genus confirmed as an ericoid mycorrhizal partner in nature. It can be distinguished from morphologically similar species, including *O. fuscum*, *O. griseum*, and the anamorphs of *M. arcticum* and *M. emodense*, by its loose head of highly undulating chains of white conidia and long conidiophores (mean >100 µm). The other species have less undulant fertile hyphae that branch at more acute angles, resulting in denser conidial heads and mean conidiophore lengths less than 100 µm. *Oidiodendron maius* var. *maius* also lacks the geniculate conidiogenesis of *M. arcticum* and the verticillate fertile hyphae of *M. emodense*.

17. *Oidiodendron muniellense* Calduch, Stchigel, Gené & Guarro, Stud Mycol 50: 161-163. 2004. **Figure 4.17**.

Colonies on decaying basidiome effuse, hairy, greenish brown, with the melanized mycelium (hyphae 1-2 µm wide, septate) partially immersed in the substrate. Colonies on OA 30-35 mm diam at four weeks at 25 °C, brownish beige to brown, flat, velvety, irregularly folded; reverse dark brown; brownish orange diffusible pigment produced. Colonies on PCA 26-30 mm diam at four weeks at 25 °C, olive-brown, flat; reverse olive brown. Colonies on PDA 37-40 mm diam at four weeks at 25 °C, grayish orange to grayish brown, slightly funiculose at center, radially folded; reverse brownish orange to yellowish brown. Conidiophores erect, melanized, up to 200 µm long, 2-3.5 µm wide; upper part bearing 4-6 verticillate appendages. Appendages several times dichotomously or trichotomously branched, straight, up to 60 µm long, 1.5-2.5 µm wide at the base, melanized, thick-walled, septate, and smooth at the base, becoming pale, thin-walled, and roughened at the pointed tips. Fertile hyphae terminal or lateral on the conidiophore apex and appendages, branched, hyaline, smooth-walled, 1-2.5 µm wide, fragmenting to form chains of conidia. Conidia globose to subglobose, ochraceous, 1.5-2.5 µm diam, covered with a reticulate network of spines as seen under SEM. Optimal growth at 25 °C. Habitat: decaying basidiome, Spain. Description from Calduch *et al.* (2004).

Notes: This species is morphologically most similar to *O. setiferum* but the appendages of *O. muniellense* are straighter than those of *O. setiferum* and are rough at the tips while those of *O. setiferum* are smooth. The conidia of *O. muniellense* are globose to subglobose and covered by a reticulate network of spines, causing them to appear asperulate to echinulate under light microscopy while those of *O. setiferum* are subglobose to ovoid or elongate with a central dimple and have a rugose perispore that causes them to appear smooth to faintly ornamented under light microscopy. Notably, the conidia of *O. tenuissimum*, which molecular evidence suggests is closely related to *O. muniellense*, are very similar: melanized, subglobose, and covered with a reticulate network of spines.

18. *Oidiodendron myxotrichoides* Calduch, Gené & Guarro, Stud Mycol 47: 217-218. 2002. **Figure 4.18**.

Colonies on beech leaves effuse, greenish brown, forming patches. Hyphae pale brown to brown, septate, branched, 1.5-2.5 µm wide. Colonies on OA 30-35 mm diam at four weeks at 15 °C, grey-violet to violet, flat, granulose; reverse dull violet to dark violet. Colonies on PCA 20-28 mm diam at four weeks at 15 °C, green-grey at the center with white to grey-white margins; reverse green-grey to dark green. Colonies on MEA 21-29 mm diam at four weeks at 15 °C, violet-grey to dark violet, velvety and radially folded; reverse violet-grey to dark violet. Colonies on PDA 28-35 mm diam at four weeks at 15 °C, grey-green, fasciculate, producing a light orange to grey-orange diffusible pigment; reverse dark brown. Conidiomata grey-green to olive, abundant, arranged in concentric circles on OA and PCA, towards the periphery on MEA, absent on PDA. Conidiomata superficial, solitary, confluent, brown to dark brown, spherical to subspherical, up to 490 µm diam, consisting of a reticulum of hyphae from which fertile hyphae are produced. Hyphae septate, brown, thick- and smooth-walled, up to 4.5 µm wide, branched and anastomosed, radially disposed. Peripheral hyphae up to 250 µm long, spine-like, straight, usually with shorter and deflected lateral branches, brown to dark brown, paling towards the apex, smooth- and thick-walled, 2-4 µm wide. Conidiophores of arborescent fertile hyphae arising laterally or terminally from the melanized hyphae of the reticulum, subhyaline, 2-3 µm wide, smooth- and thin-walled. Conidia globose, subglobose or broadly ellipsoidal, pale brown, smooth-walled or very finely rugose and thick-walled at maturity, 2-3 x 1.5-2.5 µm. Optimal growth at 15 °C; growth and sporulation reduced at 25 °C; no growth at 37 °C. Habitat: *Fagus sylvatica* leaf, Santa Fe del Montseny, Montseny Natural Park, Catalonia, Spain. Description from Calduch *et al.* (2002).

Notes: The conidiomata of *O. myxotrichoides* are described as sporodochia by Calduch *et al.* (2002); however, this term is inappropriate because the conidiomata lacks basal pads of pseudoparenchyma and do not consist of masses of short conidiophores (Hawksworth *et al.* 1995). The structure is probably best referred to simply as a conidioma. *Oidiodendron myxotrichoides* is similar to *O. hughesii* in producing conidia within a reticuloperidium-like structure but in *O. hughesii* the reticulum forms from anastomosed appendages at the apex of a solitary conidiophore while in *O. myxotrichoides* it is sessile.

19. *Oidiodendron periconioides* Morrall, Can J Bot 46: 204-205. 1968. **Figure 4.19.**

Colonies on CMA 11-18 mm diam at 28 days, dark green-grey to brown, reverse dark red-brown; orange-brown exudate produced. Conidiophores and aerial hyphae abundant. Conidia green-grey to brown *en masse*. Conidiophores smooth, melanized, and unbranched at the base, becoming hyaline and branched at apex, 25-(85)-175 x 2-4 µm. Fertile hyphae hyaline, branched, swollen to form chains of vesicles, which fragment to form chains of conidia, arising laterally from vegetative hyphae or at the conidiophore apex. Conidia thick-walled, dark, spiny at maturity, globose to ellipsoidal, 3-(3.7)-6 x 2-(3.1)-4 µm. Maximal growth at pH 3 and 20 °C. Degrades cellulose, gelatin, pectin (UAMH 6084, 8527), starch, and tannic acid.
Specimens Examined: **Canada**, Candle Lake, Saskatchewan, boreal forest soil, 1964, Morrall (UAMH 8527, *ex*-type); Nichol Springs, Cypress Hills, Alberta, root endophyte, *Calypso bulbosa* (L.) Oakes, May 1987, Hambleton (UAMH 6084); **Japan**, humus, Currah (UAMH 7289).

Notes: *Oidiodendron periconioides* is unique in the genus because it produces chains of globose, vesicle-like, swellings that precede the appearance of conidia in short conidiogenous branches. It is the only species of *Oidiodendron* that consistently produces dark, spiny, globose to ellipsoidal conidia. *Oidiodendron echinulatum* is similar but has ellipsoidal conidia, rounded warts on the perispore, and is WDG positive while *O. periconioides* is WDG negative.

20. *Oidiodendron pilicola* Kobayasi, Bulletin of the National Sciences Museum (Tokyo) 12: 424-425. 1969. **Figure 4.20.**

Conidiophores simple, erect, septate, thick-walled, pale olivaceous brown, 100-150 x 2.5-4 µm. Upper part branched monopodially (laterally and oppositely) into fertile hyphae. Fertile hyphae (1.5-2.5 µm diam), 2-3 x branched, hyaline, fragmenting to form conidia. Conidia hyaline, barrel-shaped, truncate with frills at both ends, smooth, catenate, apically or laterally produced, forming dense clusters, 3-3.5 x 1.5-2 µm. Habitat: human hair, soil. Description from Kobayasi (1969).

Specimen Examined: **Sweden**, forest soil, 1972, Nylund (UAMH 7526). Degenerate and not producing conidia.

Notes: *Oidiodendron pilicola* resembles *O. truncatum* and the anamorphs of *M. cancellatum* and *M. striatosporum* in producing barrel-shaped conidia that are truncate at both ends. Conidia of *O. pilicola* are hyaline, while those of *O. truncatum* and *M. striatosporum* are dark, and are smooth compared to those of *O. truncatum* and *M. cancellatum*, which are reticulate and *M. striatosporum* which are asperulate. Molecular evidence suggests that this species is distinct but close to *O. chlamydosporicum* (Hambleton, unpublished).

21. *Oidiodendron rhodogenum* Robak, Saertryk av Nyt Mag Naturvidensk 71: 251-255. 1932. **Figure 4.21.**

Colonies on CMA 31-34 mm diam at 28 days, off-white to grey, appressed; reverse brown to grey brown. Red diffusible pigment absent on CMA but produced by UAMH 1405 on OA. Conidiophores abundant, bearing masses of off-white to pale green conidia, smooth, branched, melanized, 30-(50)-85 x 3-6 µm. Fertile hyphae hyaline, 2-5 µm diam, dichotomously branched, fragmenting into long chains of conidia. Conidia hyaline to lightly pigmented, subglobose to elongate and irregular, 1.5-(2.5)-5 x 1.5-(1.6)-2 µm, with a rugose perispore and visible dehiscence scars. Maximal growth at pH 3 and 20 °C. Degrades cellulose, gelatin, pectin, and starch.

Specimens Examined: **Norway**, Kistefoss Mills, sludge in pulp strainers, 1929, Robak (UAMH 1405, authentic); **Canada**, Ontario, forest soil, 1969, Barron (CBS 401.69 = UAMH 8508).

Notes: *Oidiodendron rhodogenum* has been identified traditionally on the basis of a red diffusible pigment in culture but this character is unreliable; pigment production is inconsistent within and among isolates. In the absence of the red pigment, *O. rhodogenum* is difficult to identify because, although the species physlogenetically distinct, it is not distinctive morphologically or on the basis of single substrate tests. Additional enzymatic characters (Rice & Currah, in press 1) indicate the physiological distinctiveness of this species. *Oidiodendron fuscum* and *O. griseum* are similar but have unbranched conidiophores. In addition, the conidia of *O. rhodogenum* are elongate to cylindrical with a rugose perispore under SEM while those of *O. griseum* are asperulate, and those of *O. fuscum* are dimpled, asperulate, and subglobose to ellipsoidal.

22. *Oidiodendron setiferum* Udagawa & Toyazaki, Mycotaxon 28: 234-238. 1987. **Figure 4.22**.
= *Oidiodendron ramosum* Calduch, Stchigel, Gené & Guarro

Colonies on CMA 23-25 mm diam at 28 days, brown, appressed; reverse green-grey to black (darkest under areas of conidial production). Conidiophores abundant, bearing masses of conidia and appendages, smooth, melanized, branching at apex to form appendages and fertile hyphae, 40-(80)-180 x 2-3 µm. Fertile hyphae hyaline, penicillate, borne either at the conidiophore apex or at the tips or branching points of the appendages, and forming a dense head of conidia. Appendages (2-4 per conidiophore) produced at the apices of the conidiophores and subtending masses of conidia, dichotomously branched, melanized, with tapered apices, often curved or recurved, 20-100 x 2-3 µm. Conidia thin-walled, hyaline to lightly melanized, subglobose to ellipsoidal, elongate or irregular, 1.5-(2.5)-4 x 1-(1.5)-2.5 µm, with a rugose perispore and central dimple under SEM. Maximal growth at pH 3 and 25 °C. Degrades cellulose, gelatin, pectin, starch, and tannic acid.
Specimen Examined: **Japan**, Kobe, house dust, Udagawa (UAMH 5715, *ex*-type).

Notes: Calduch *et al.* (2004) distinguished *O. ramosum* from *O. setiferum* on the basis of the fertility of the appendages and on conidial ornamentation. *Oidiodendron setiferum* was described as having sterile appendages surrounding the fertile head (Udagawa & Toyazaki 1987) while in *O. ramosum*, the appendages often give rise to fertile hyphae from their branching points or apices (Calduch *et al.* 2004). Although not noted in the original description, my SEM observations of the *ex*-type of *O. setiferum* show that fertile hyphae and conidia do arise from the branching points and apices of the appendage. The conidia of *O. ramosum* are described as smooth to slightly roughened (Calduch *et al.* 2004) and those of *O. setiferum* as smooth (Udagawa & Toyazaki 1987). However, SEM examination of *O. setiferum* shows that the conidia have a rugose perispore and are as roughened as the conidia of *O. ramosum* as shown in the SEM images provided by Calduch *et al.* (2004). Thus, the differences noted by Calduch *et al.* (2004) between the original description of *O. setiferum* and their taxon, *O. ramosum*, cannot be substantiated and *O. ramosum* is here considered a synonym of *O. setiferum*. The two taxa group together based on ITS sequence data (Calduch *et al.* 2004). While the low bootstrap support (54) for that group suggests some distinctiveness, without information about the percent of genetic difference between them, it is insufficient to rule out synonymy.

Oidiodendron setiferum, *O. muniellense*, and *O. hughesii* can be distinguished from others in the genus by the melanized appendages that subtend the arthroconidia. See notes under *O. hughesii* and *O. muniellense*.

23. *Oidiodendron tenuissimum* (Peck) Hughes, Can J Bot 36: 790. 1958. **Figure 4.23.**

≡*Periconia tenuissima* Peck *fide* Hughes (1958)

Colonies on CMA 18-22 mm diam at 28 days, pale brown, appressed; reverse dark grey-brown to black. Conidiophores abundant, arranged in concentric circles, bearing masses of brown conidia, unbranched, melanized, 30-(95)-240 x 2-4 µm. Fertile hyphae hyaline, dichotomously branched, fragmenting to form chains of conidia. Conidia melanized at maturity, faintly ornamented, subglobose to elongate, 2-(2.5)-4 x 1-(2.1)-3 µm, covered by a reticulate network of spines as revealed by SEM. Maximal growth at pH 3-5 and 20 °C. Degrades cellulose, gelatin, lipid, pectin, and starch.

Specimens Examined: **Spain**, La Gomera, Canary Islands, leaf litter, 1995, Castañeda (UAMH 8513); **Canada**, Guelph, Ontario, soil, mixed deciduous forest, 1960, Barron (UAMH 1523).

Notes: See also notes under *O. fuscum* and *O. griseum*. Both UAMH 8513 and 1523 had been identified as *O. tenuissimum sensu* Barron, but were subsequently considered distinct on the basis of ITS sequences and were labeled "*O.* sp. nov." (Hambleton *et al.* 1998). Comparison of these isolates with type material of *Periconia tenuissima* show that the three isolates are indistinguishable and are best accommodated under the name *O. tenuissimum*. *Oidiodendron tenuissimum* has brown colonies, conidiophores that may exceed 200 µm, and dark, spinulose conidia as opposed to the off-white or pale grey colonies, shorter conidiophores (less than 100 µm long), and hyaline, minutely verruculose to asperulate conidia of *O. fuscum*. It can be distinguished from other species of *Oidiodendron* by the dark, subglobose to ellipsoidal or elongate conidia with a network of spines.

24. *Oidiodendron truncatum* Barron, Can J Bot 40: 602-604. 1962. **Figure 4.24.**

Colonies on CMA 30-32 mm (UAMH 8443) to 38-42 mm (UAMH 1399, 10464) diam at 28 days, brown to green-grey, appressed; reverse green-grey to brown. Conidiophores abundant, clumped, bearing masses of brown conidia, smooth, branched at apex, more or less melanized, 18-(75)-180 x 2-4 µm. Conidia dark at maturity, produced in branched chains at the conidiophore apex or from vegetative hyphae, barrel-shaped to irregular, truncate with distinct apical scars and reticulate ornamentation, 2-(3.6)-5 x 1-(2.5)-3.5 µm. Maximal growth at pH >7 and 15-20 °C. Degrades cellulose, gelatin, lipid, and pectin.
Specimens Examined: **Canada**, Guelph, Ontario, soil, mixed forest, 1960, Barron (UAMH 1399, *ex*-type); Slave Lake, Alberta, decaying spruce wood, Lumley (UAMH 10464); **Italy**, soil of snow valley, Mosca (UAMH 8443 = ATCC 36256, as *O. ambiguum*).

Notes: This species can be readily distinguished from others in the genus because of its dark, reticulately ornamented, barrel-shaped, truncate conidia and its inability to degrade starch.

4.6. Excluded Species

Oidiodendron robustum Mercado Sierra & Casteñeda Ruiz, Acta Botanic Cubana 33: 3-4. 1985.

The type specimen for this species was not examined but its conidiophores that are described as 250-870 x 7.5-10.5 µm and conidia 5-11 x 2.5-3.2 µm (Mercado Sierra & Casteñeda Ruiz 1985). Both are much larger than is found in all other species of *Oidiodendron* and are more reminiscent of species of *Cladosporium*. From the original illustrations and description it is impossible to determine whether the chains of conidia are forming by basipetal fragmentation or acrogenous budding. Based on these ambiguities, this taxon is excluded from the genus.

Oidiodendron terrestre Roy & Singh, J Indian Bot Soc 48: 158-159. 1969.

This species is described as having rapid growth (90 mm in 3 days), hyaline conidiophores, chlamydospores 4.5-14 x 3.5-12.5 µm, and ellipsoidal to cylindrical, one-to-two celled conidia 4-15 x 3-13 µm (Roy & Singh 1969). This growth rate is much greater, and conidia much larger than observed in other *Oidiodendron* species. In addition, two-celled conidia are inconsistent with the generic diagnosis. Conidial ontogeny is unclear from the original description and illustrations but appears blastic and acropetal rather than basipetal. The absence of definitive *Oidiodendron* characters, along with the large, two-celled conidia, rapid growth, and hyaline conidiophore, easily exclude this species from *Oidiodendron*.

Table 4.1: Sources and enzymatic profiles for *Oidiodendron* isolates studied.

Species	Strain	Source	CEL	GEL	LIP	PEC	STA	TAM	WDG
Myxotrichum arcticum	UAMH 7565[t]	Forest soil, USA	+	+	-	+	+	+	-
M. arcticum	UAMH 9243	Decayed spruce, Canada	+	+	-	+	+	-	-
M. cancellatum	UAMH 1996	Soil, Japan	-	+	-	+	+	-	-
M. setosum	UAMH 3835	Soil, Canada	-	+	+	+	+	-	-
M. setosum	UAMH 4535	Washed mineral soil, Canada	-	+	+	+	+	-	-
Oidiodendron cerealis	UAMH 504	Human hair, Canada	+	+	-	+	+	-	-
O. cerealis	UAMH 1522	Peat soil, Canada	+	+	-	+	+	-	-
O. cerealis	CBS 349.62	Soil, Italy	+	+	-	+	+	-	-
O. chlamydosporicum	UAMH 6520[t]	Soil, Canada	+	+	+	+	+	-	+
O. chlamydosporicum	UAMH 6521[t]	Soil, Sweden (*O. scytaloides*)	+	+	-	+	+	-	+
O. chlamydosporicum	UAMH 6527	Soil, Sweden (*O. scytaloides*)	+	+	-	+	+	-	-
O. chlamydosporicum	UAMH 8510	Fir roots, Germany (*O. scytaloides*)	+	+	+	+	+	-	-
O. chlamydosporicum	UAHM 9751	*Sphagnum*, Canada (*O. scytaloides*)	+	+	+	+	+	+	-
O. echinulatum	UAMH 8467[a]	Peat soil, Canada	+	+	+	-	+	+	+
O. fimicolum	UAMH 10459[t]	Mushroom compost, USA	NA	NA	NA	NA	NA	NA	NA
O. fimicolum	UAMH 10523	Mushroom compost, USA	NA	NA	NA	NA	NA	NA	NA
O. flavum	UAMH 1524[a]	Peat soil, Canada	+	+	+	+	+	-	-
O. fuscum	UAMH 8511[t]	Wood pulp, Norway	-	+	+	+	+	-	-
O. griseum	UAMH 1403[a]	Wood pulp, Norway	+	+	-	+	+	+	-
O. griseum	UAMH 4080	Wood chips, Canada	+	+	-	+	+	+	-

O. griseum	UAMH 8925	*Vaccinium* roots, Canada	+	+	-	+	+	+	-
O. maius var. *citrinum*	UAMH 1525	Cedar bog soil, Canada	+	+	+	+	+	+	+
O. maius var. *citrinum*	UAMH 7089	*Ex* sclerotia, stream drift, Canada	+	+	+	+	+	+	+
O. maius var. *citrinum*	UAMH 9275	*Ex* mycorrhizal root tip, Canada	+	+	+	+	+	+	+
O. maius var. *maius*	UAMH 1540[t]	Peat soil, Canada	+	+	+	+	+	+	-
O. maius var. *maius*	UAMH 8920	*Oxycoccus* roots, Canada	+	+	+	+	+	+	-
O. maius var. *maius*	UAMH 9749	Decaying *Sphagnum*, Canada	+	+	+	+	+	+	-
O. maius var. *maius*	UAMH 10460	*Vaccinium* roots, Canada	+	+	+	+	+	+	-
O. maius var. *maius*	UAMH 10461	*Vaccinium* roots, Finland	+	+	+	+	+	+	-
O. periconioides	UAMH 6084	*Calypso* roots, Canada	+	+	-	+	+	+	-
O. periconioides	UAMH 7289	Humus, Japan (*O. echinulatum*)	+	+	-	-	+	+	-
O. periconioides	UAMH 8527[t]	Soil, Canada	+	+	-	+	+	+	-
O. rhodogenum	UAMH 1405[a]	Pulp sludge, Norway	+	+	-	+	+	-	-
O. rhodogenum	CBS 401.69	Soil, Canada	+	+	-	+	+	-	-
O. setiferum	UAMH 5715[t]	House dust, Japan	+	+	-	+	+	+	-
O. tenuissimum	UAMH 1523	Forest soil, Canada	+	+	+	+	+	-	-
O. tenuissimum	UAMH 8513	Leaf litter, Spain	+	+	+	+	+	-	-
O. truncatum	UAMH 1399[t]	Forest soil, Canada	+	+	+	+	-	-	-
O. truncatum	UAMH 8443	Soil, Italy (*O. ambiguum*)	+	+	+	+	-	-	-
O. truncatum	UAMH 10464	Decaying spruce, Canada	+	+	+	+	-	-	-

CEL = cellulose azure, GEL = gelatin, LIP = TWEEN 20 (lipid), PEC = pectin, STA = starch, TAM = tannic acid medium, WDG = wood guaiacol (lignin), [t] = *ex* type, [a] = authentic, + = positive reaction, - = negative reaction, NA = not tested

Table 4.2: Conidial shapes in *Oidiodendron* species.

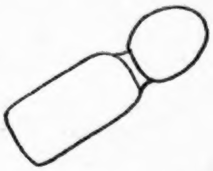
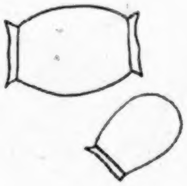
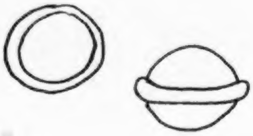
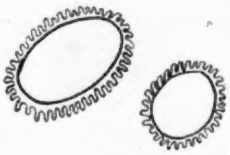
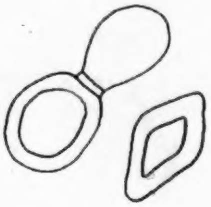
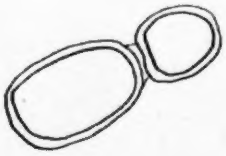
Conidial shape	Illustration	Species
Subglobose to elongate, thin-walled, with indistinct ornamentation		*Myxotrichum arcticum, M. emodense, M. setosum, Oidiodendron chlamydosporicum, O. fuscum, O. griseum, O. maius, O. setiferum , O. rhodogenum*
Barrel-shaped, truncate, with distinct dehiscence scars		*M. cancellatum, M. striatosporum, O. pilicola, O. truncatum*
Lens-shaped with a thickened ring		*O. cerealis*
Globose to ellipsoidal, thick-walled, echinulate		*O. echinulatum, O. muniellense, O. periconioides*
Pyriform to irregular, thick walls, with indistinct to asperulate ornamentation (not discernable at this scale)		*O. fimicolum, O. flavum*
Subglobose to elongate, thick-walled, with indistinct to asperulate ornamentation (not discernable at this scale)		*O. fimicolum, O. flavum, O. hughesii, O. myxotrichoides, O. tenuissimum*

Figure 4.1. *Oidiodendron* anamorph of *Myxotrichum arcticum*.

A. Small, dense head of subglobose to elongate, hyaline conidia at the apex of a tall, erect, melanized conidiophore (UAMH 7565). Bar = 20 µm. **Inset**. "Geniculate conidiogenesis." Conidiophore apex bearing whorls of truncated chains of one to two conidia. Arrow indicates connectives between two conidia in a chain; arrowheads indicate scars from detached conidia. Bar = 2.5 µm. Reproduced with permission from Tsuneda & Currah 2004 (Figure 28). **B**. Branches of fertile hyphae fragmenting to form subglobose to elongate, asperulate to spinulose conidia (UAMH 9243). Bar = 10 µm. **C**. Chains of asperulate to spinulose, subglobose to elongate conidia with short connectives visible between them (UAMH 9243). Bar = 1 µm.

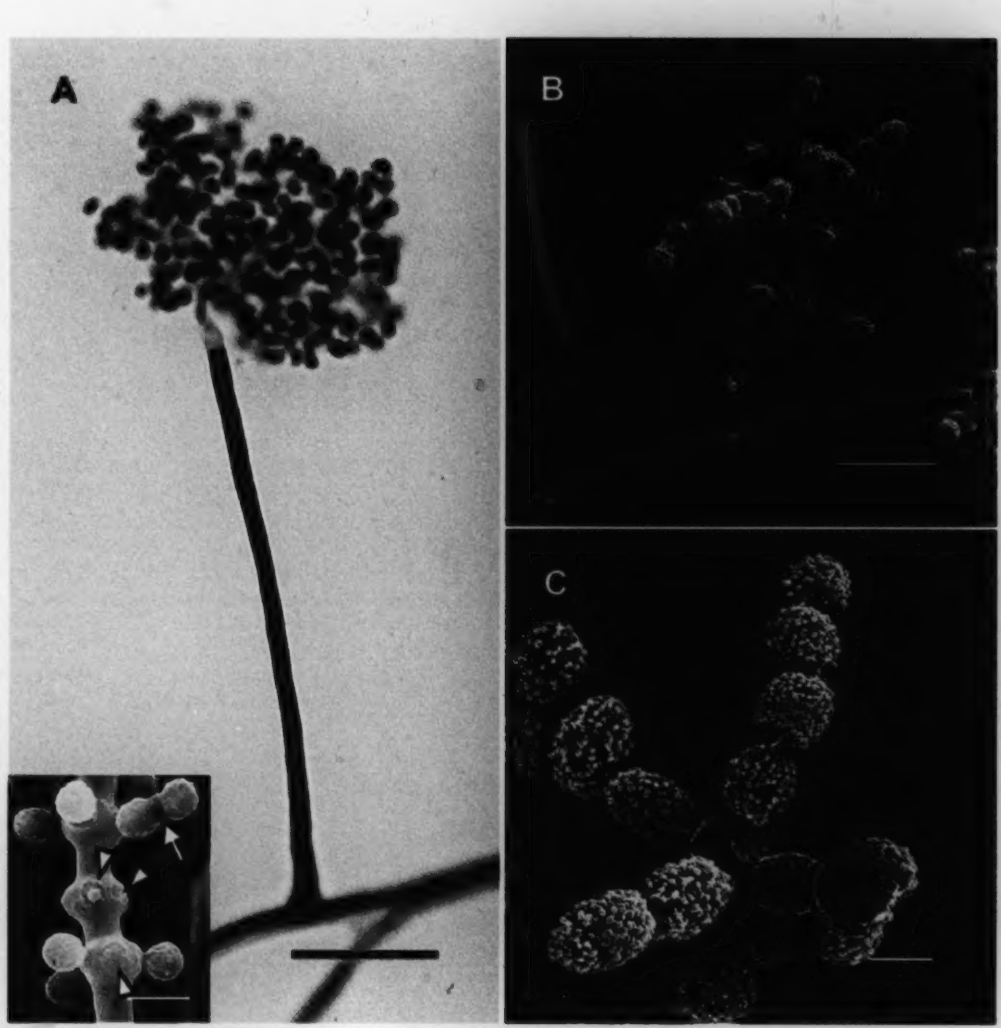

A
B
C

Figure 4.2. *Oidiodendron* anamorph of *Myxotrichum cancellatum* (UAMH 1996).

A. Short, erect conidiophores bearing divergent chains of thick-walled, hyaline to lightly pigmented, barrel-shaped conidia. Bar = 15 µm. **B**. Conidiophores bearing long chains of subglobose to barrel-shaped conidia. Bar = 10 µm. **C**. Subglobose to barrel-shaped conidia with a rugose to reticulate perispore. Bar = 1 µm.

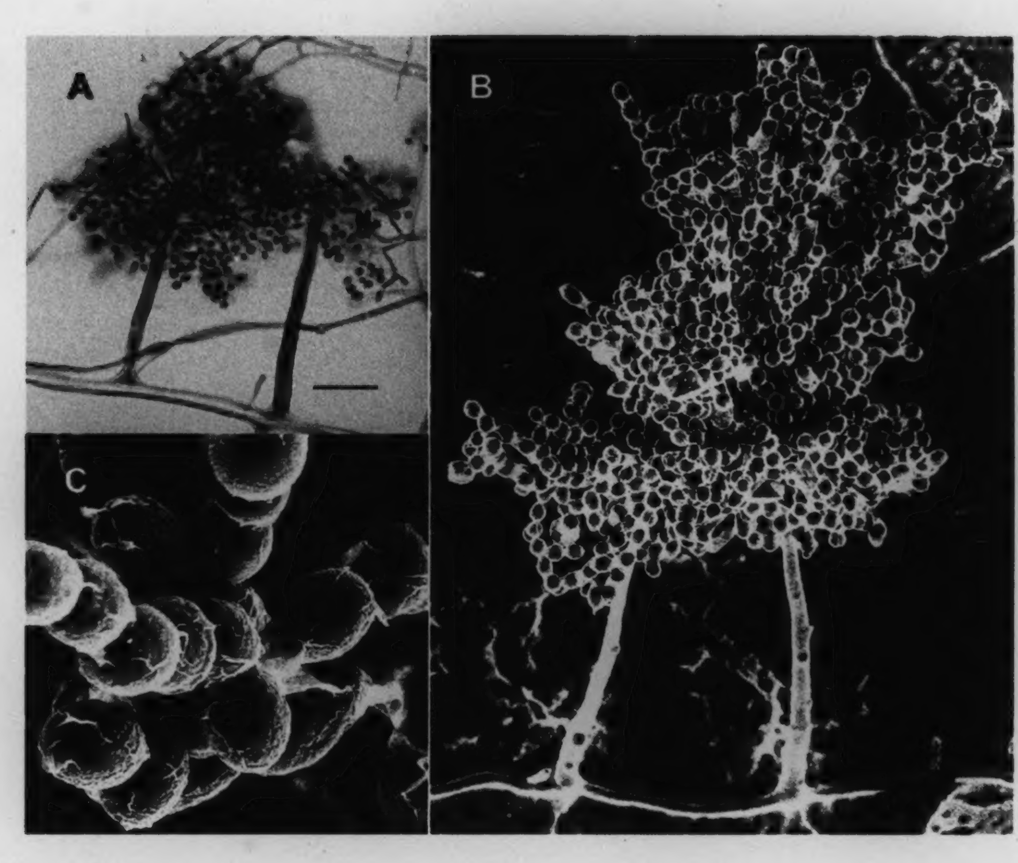

A
B
C

Figure 4.3. *Oidiodendron* anamorph of *Myxotrichum emodense*. Light micrographs reproduced with permission from Udagawa & Uchiyama 1999 (Figures 13, 14).

A. Dichotomously branched conidiophore bearing verticillate whorls of fertile hyphae that give rise to subglobose to ellipsoidal and elongate conidia. Bar = 20 µm. **B**. Divergent branches of a conidiophore give rise to verticils of fertile hyphae and thick-walled, subglobose to ellipsoidal conidia. Bar = 20 µm.

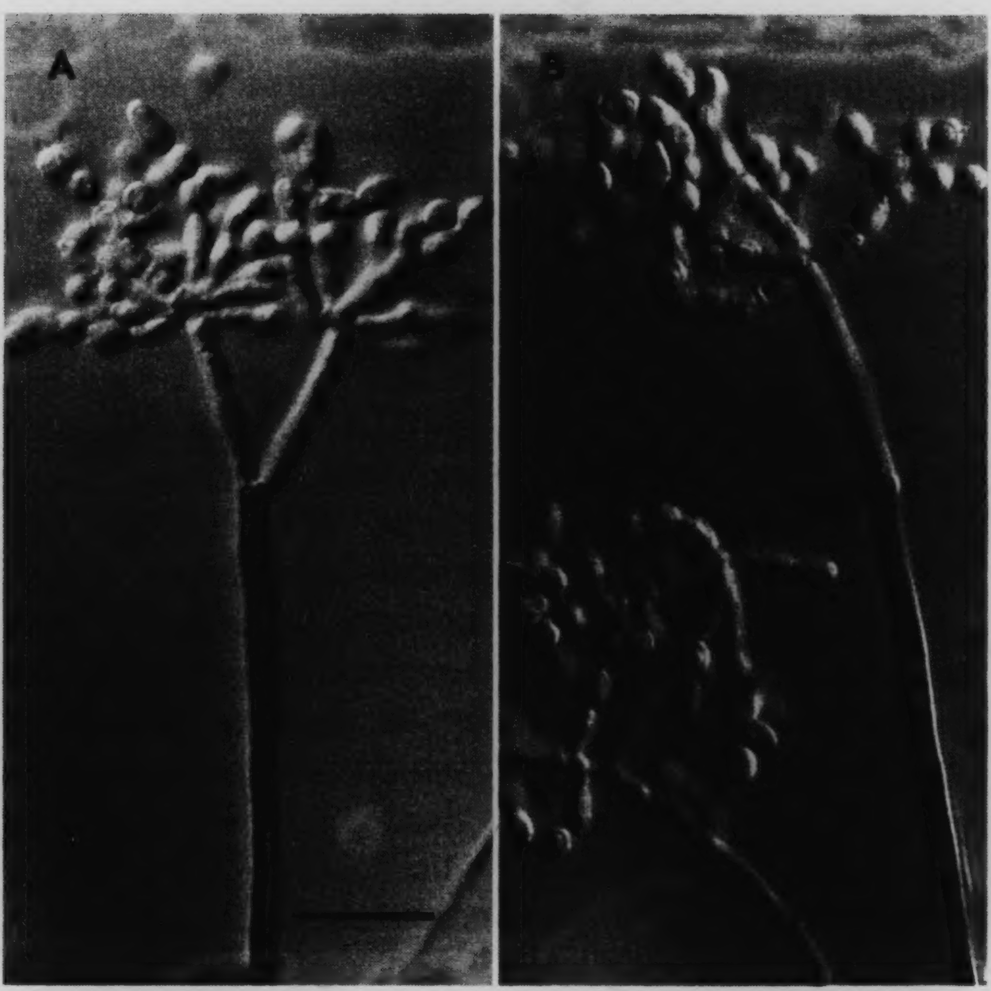

A
B

Figure 4.4. *Oidiodendron* anamorph of *Myxotrichum setosum* (UAMH 3835).

A. Short, sparingly branched chains of elongate conidia produced from vegetative hyphae. Bar = 10 µm. **B**. Chains of elongate conidia that collapse upon desiccation. Bar = 5 µm. **C**. Short, unbranched chain of elongate conidia. Bar = 5 µm.

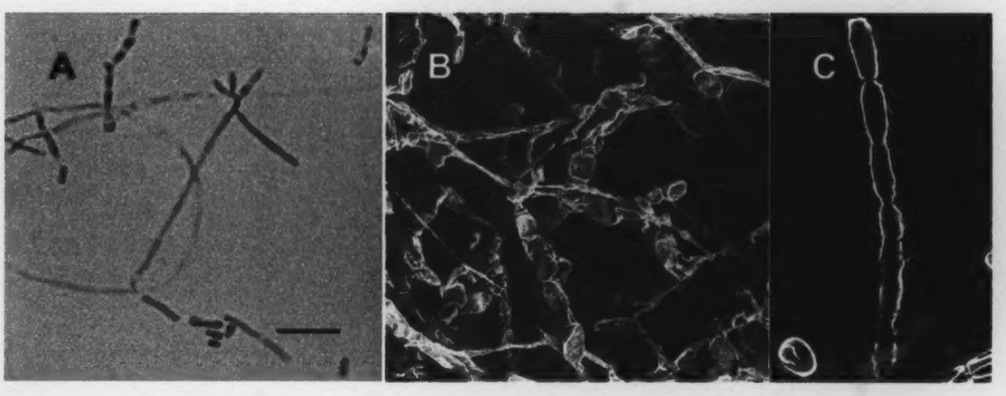

A
B
C

Figure 4.5. *Oidiodendron* anamorph of *Myxotrichum striatosporum* (UAMH 3758).

A. Conidiophores arising from a melanized section of the vegetative hyphae. The melanized lower portions of the conidiophores are unbranched and give rise to much longer, hyaline upper portions that branch several times and bear fertile hyphae. Fertile hyphae fragment to form lightly pigmented to melanized, smooth to asperulate, thick-walled, barrel-shaped, truncate conidia with apical scars. Bar = 15 µm. **B**. Long chains of lightly pigmented to melanized, smooth to asperulate, thick-walled, barrel-shaped to rectangular conidia with darker apical scars. Bar = 15 µm.

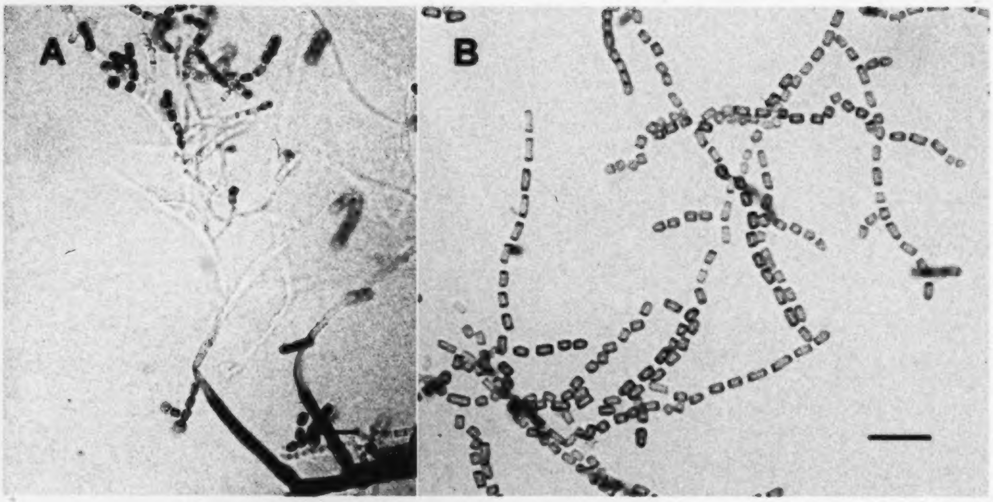

A
B

Figure 4.6. Tall conidiophore of *Oidiodendron ambiguum* bearing branched fertile hyphae and verruculose, subglobose to ellipsoidal conidia. Bar = 20 µm. Reconstructed from the descriptions and illustrations of Peyronel (1914) and Malan (1949).

4.6

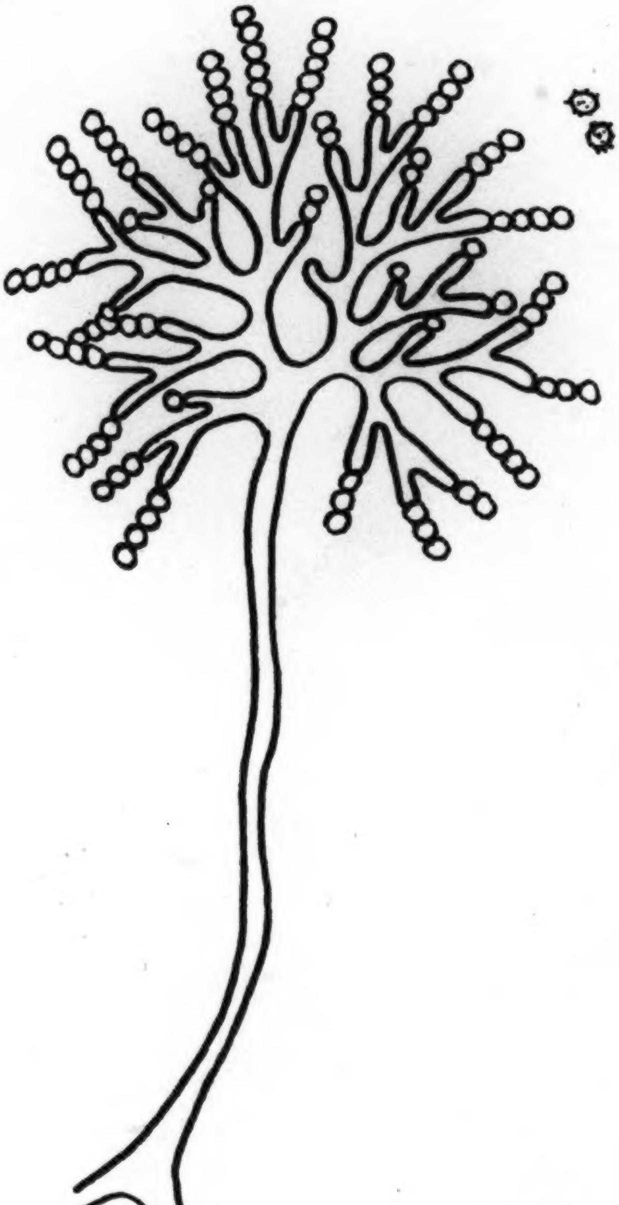


Figure 4.7. *Oidiodendron cerealis* (UAMH 1522).

A. Dark, lens-shaped conidia produced in clusters at the apices of short, hyaline to lightly pigmented conidiophores. Bar = 10 µm. **B**. Short conidiophores branched at the apices and supporting chains of lens-shaped conidia with an extremely rugose perispore. Bar = 1 µm. **C**. Lens-shaped conidia with a rugose perispore. Bar = 1 µm.

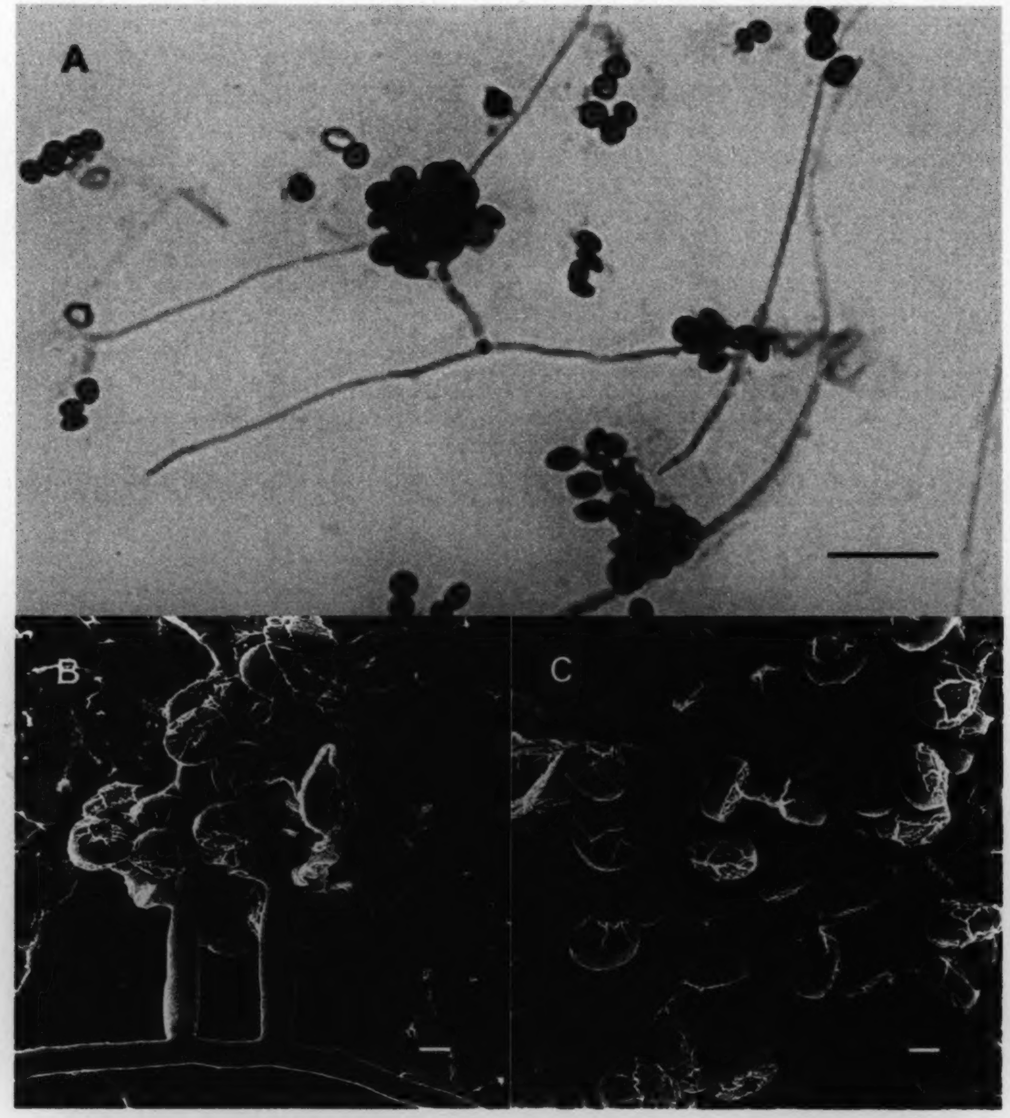

A
B
C

Figure 4.8. *Oidiodendron chlamydosporicum.*

A. Elongate, hyaline conidia produced in short chains at the apices of short, dark conidiophores and lateral, terminal, and intercalary, dark, subglobose to elongate or irregular chlamydospores produced singly or in short chains, from vegetative hyphae (UAMH 9751). Bar = 10 µm. **B**. Asperulate, elongate conidia (C) in short chains at a conidiophore apex; intercalary, pitted chlamydospores (arrowhead) borne on a vegetative hypha (UAMH 6520). Bar = 1 µm.

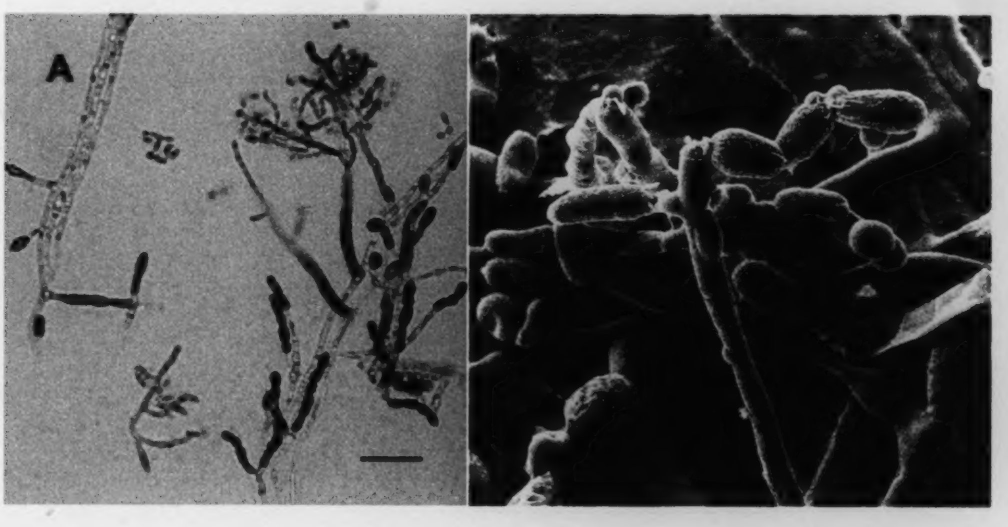

A

Figure 4.9. *Oidiodendron echinulatum* (UAMH 8467).

A. Erect conidiophore bearing divergent, branched chains of thick-walled, warty, dark, subglobose to ellipsoidal conidia. Bar = 15 µm. **B**. Subglobose to ellipsoidal, warty or pitted conidia. Short connectives are visible between some conidia. Bar = 1 µm.

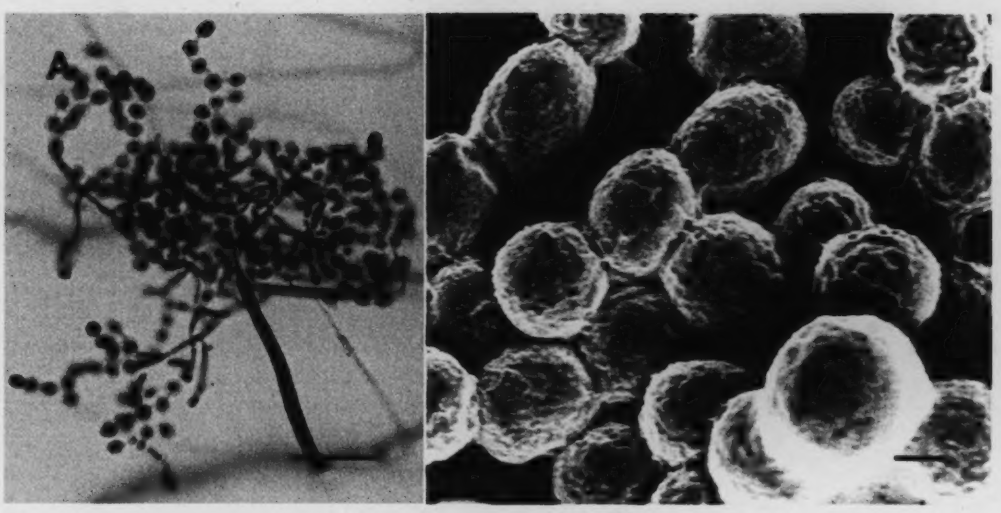

A

Figure 4.10. *Oidiodendron fimicolum* (UAMH 10459).

A. Short, asperulate conidiophores bearing short chains of thick-walled, lightly pigmented to dark, barrel-shaped to elongate or irregular conidia. Bar = 15 µm. **B**. Portion of fertile hypha bearing chains of asperulate, subglobose to elongate or barrel-shaped conidia with long, thing connectives visible between conidia. Bar = 5 µm. **C**. Fragment of scaly conidiophore and asperulate, elongate to irregular conidia with the remnants of connectives remaining at their apices. Bar = 1 µm.

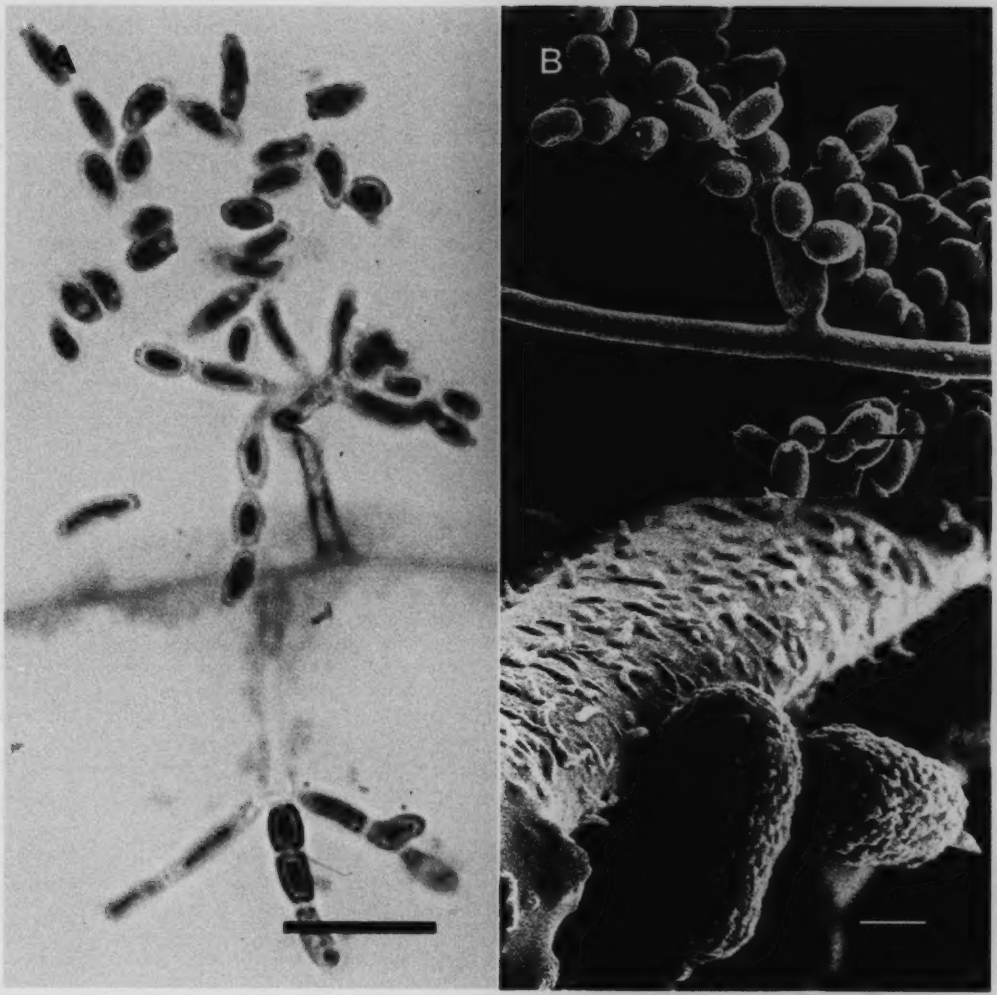

A
B

Figure 4.11. *Oidiodendron flavum* (UAMH 1524).

A. Erect conidiophores bearing short chains of thick-walled, lightly pigmented to dark, pyriform to irregular conidia. Bar = 15 µm. **B**. Smooth to pitted, subglobose to pyriform conidia borne on fertile hyphae. Bar = 1 µm. **C**. Smooth to pitted, subglobose to pyriform or irregular conidia. Bar = 1 µm.

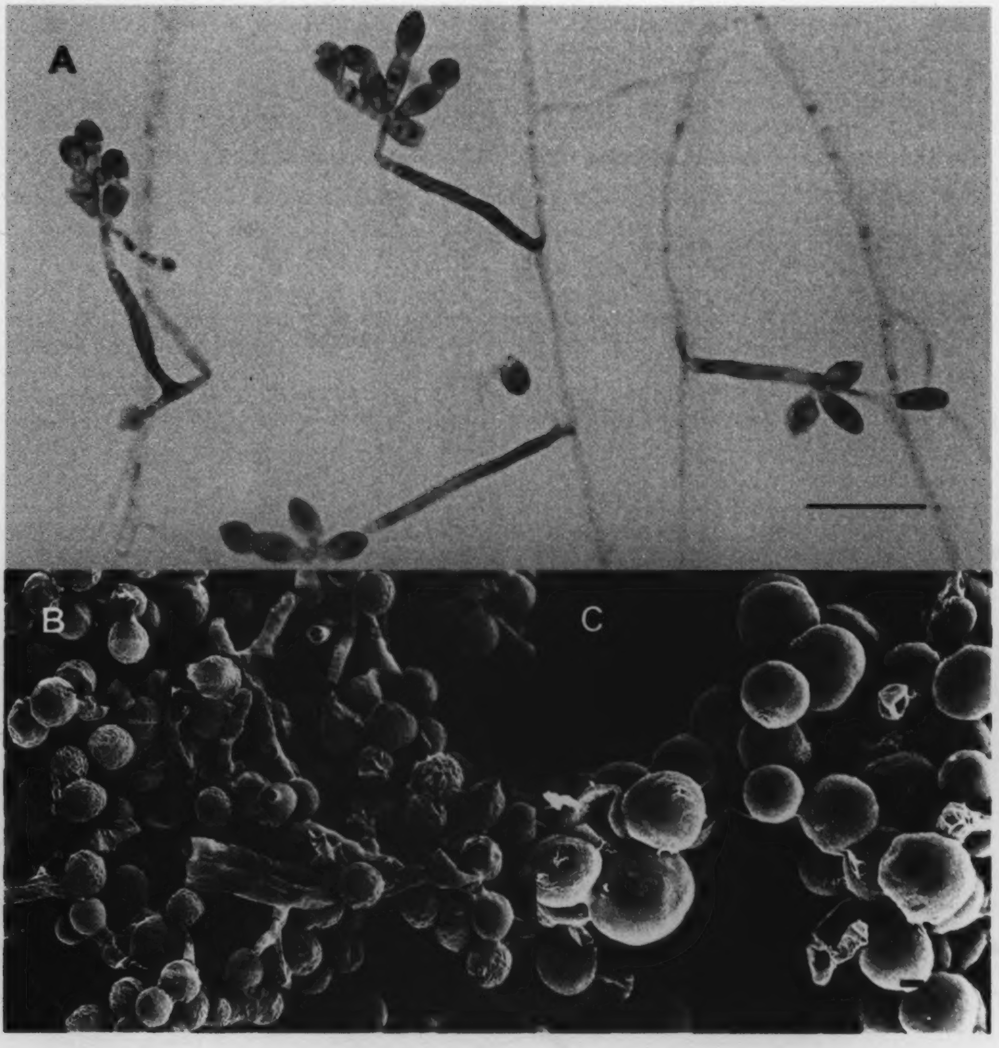

A
B
C

Figure 4.12. *Oidiodendron fuscum* (UAMH 8511).

A. Tall, erect conidiophore bearing a dense head of thin-walled, subglobose to ellipsoidal conidia. Bar = 15 µm. **B**. Conidiophores bearing a large, dense head of dimpled, asperulate, subglobose conidia. Bar = 10 µm. **C**. Short chain of subglobose to ellipsoidal, dimpled, asperulate to minutely verruculose conidia. Long connectives are visible between conidia. Bar = 1 µm.

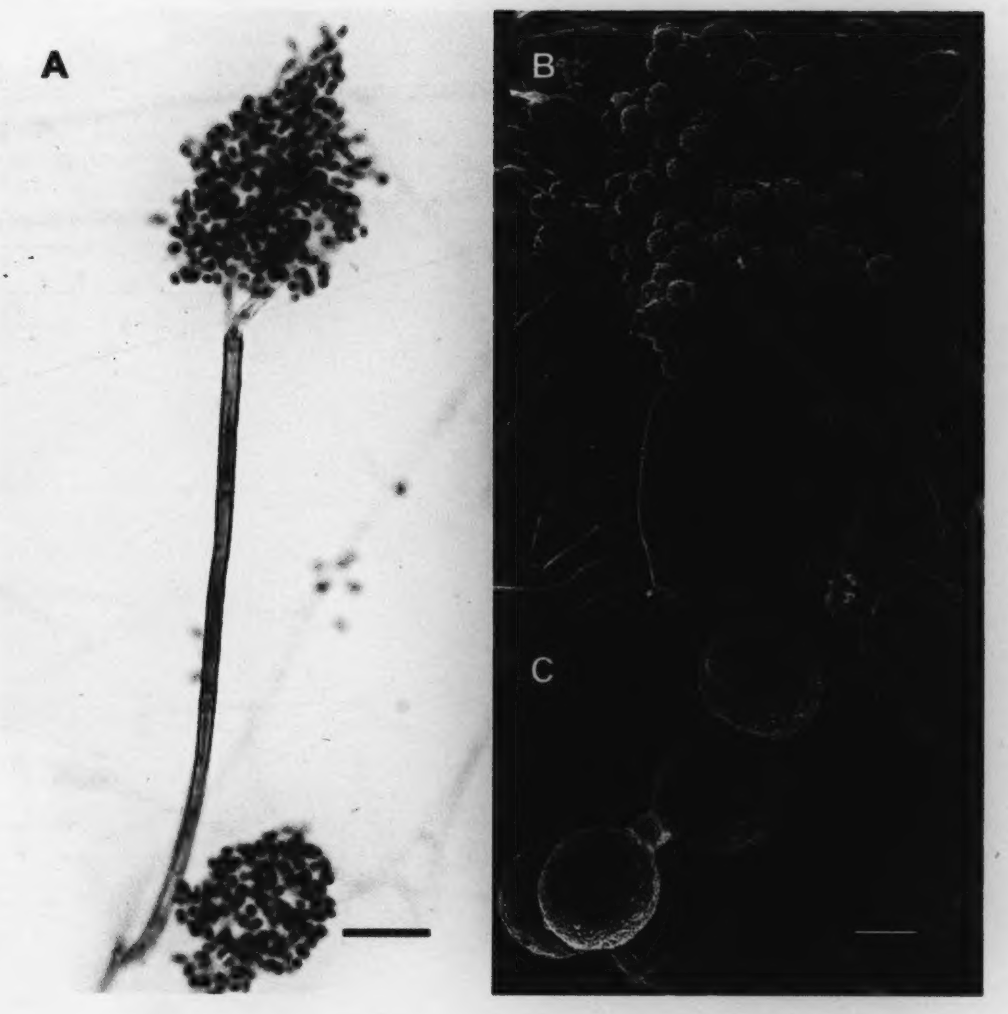

A
B
C

Figure 4.13. *Oidiodendron griseum*.

A. Conidiophore bearing long chains of elongate to cylindrical conidia (UAMH 1403). Bar = 15 µm. **B**. Chains of asperulate, subglobose to elongate or cylindrical conidia with short connectives visible between some of the conidia (UAMH 4080). Bar = 5 µm. **C**. Asperulate, subglobose to elongate and cylindrical conidia with connectives visible between some of the conidia (UAMH 4080). Bar = 5 µm.

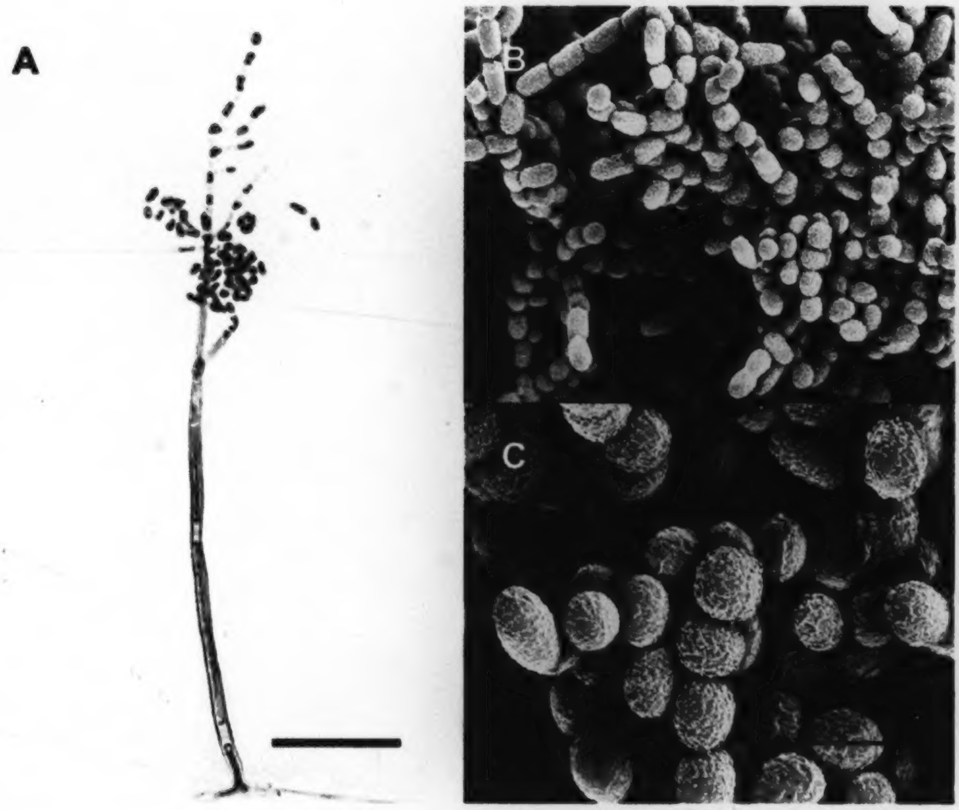

A
B
C

Figure 4.14. *Oidiodendron hughesii*. Reproduced with permission from Udagawa & Uchiyama 1998 (Figures 11, 14, 17) and Calduch *et al.* 2004 (Figures 24, 27, 31).

A. Conidiophore and reticulum of asperulate appendages surrounding a conidial mass (*O. reticulatum*; Calduch *et al.* 2004, Figure 24). Bar = 30 µm. **B**. Conidiophore and reticulum of smooth to asperulate appendages surrounding a conidial mass (*O. hughesii*; Udagawa & Uchiyama 1998, Figure 11). Bar = 50 µm. **C**. Simple conidiophore bearing chains of asperulate to spinulose, ellipsoidal conidia (*O. hughesii*; Udagawa & Uchiyama 1998, Figure 17). Bar = 10 µm. **D**. Appendages of the reticulum surrounding the conidial mass. Note that the asperulate ornamentation does not extend to the apices (*O. hughesii*; Udagawa & Uchiyama 1998, Figure 14). Bar = 50 µm. **E**. Asperulate hyphae of the reticulum surrounding the conidial mass. Note that the asperulate ornamentation of the hyphae extends almost to the apices but that the tips of the hyphae are still smooth (*O. reticulatum*; Calduch *et al.* 2004, Figure 27). Bar = 10 µm. **F**. Ellipsoidal, asperulate to spinulose conidia (*O. reticulatum*; Calduch *et al.* 2004, Figure 31). Bar = 2 µm.

✓

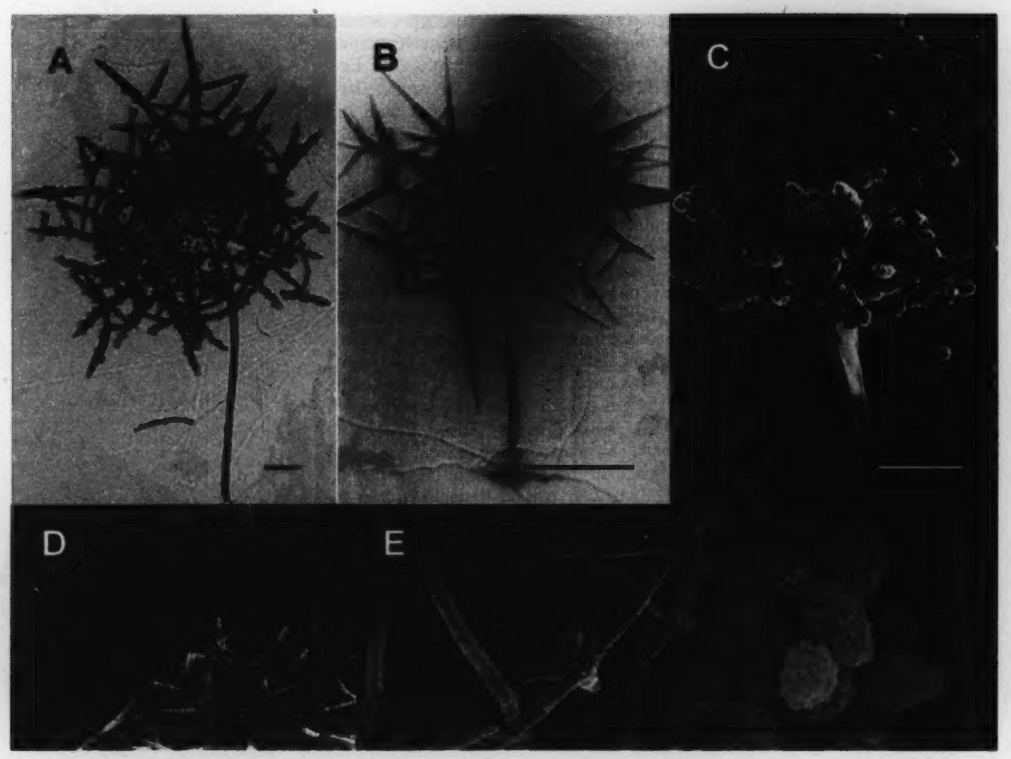

A
B
C
D
E

Figure 4.15. *Oidiodendron maius* var. *citrinum* (UAMH 1525).

A. Tall, erect conidiophore bearing a branched head of fertile hyphae that fragment to form long chains of subglobose to elongate conidia. Bar = 15 µm. **B**. Subglobose to elongate conidia with a rugose perispore. Bar = 1 µm.

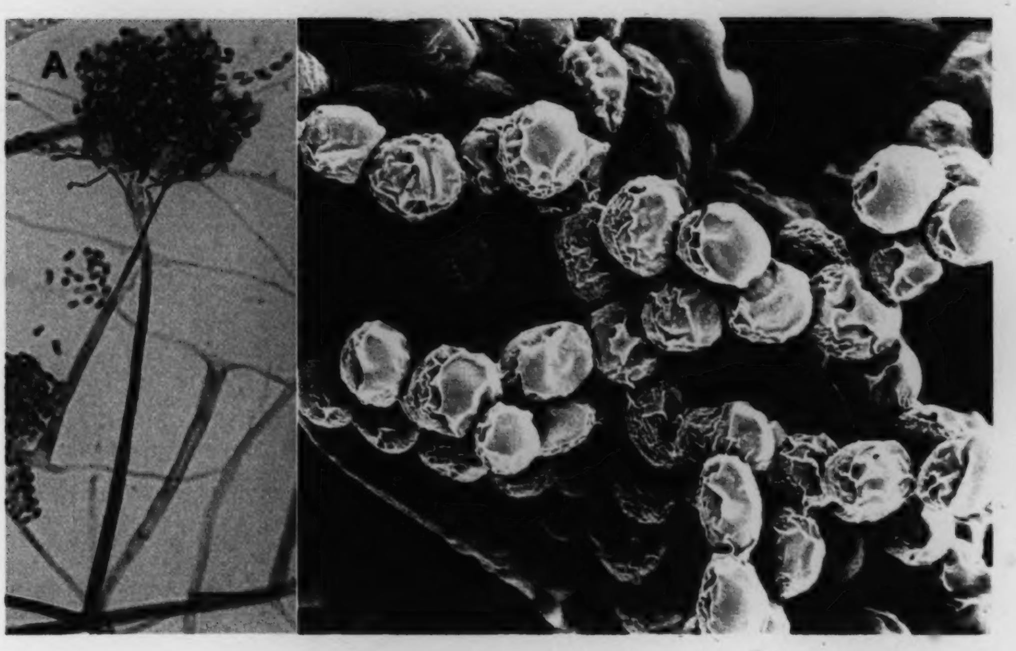

A

Figure 4.16. *Oidiodendron maius* var. *maius*.

A. Extremely tall conidiophore bearing a head of divergent, branched, undulating chains of thin-walled, subglobose to elongate or cylindrical conidia (UAMH 9749). Bar = 40 µm. **B**. Conidiophore apex branching to form fertile hyphae that fragment to form chains of subglobose to elongate conidia (UAMH 10460). Bar = 10 µm. **C**. Chains of asperulate, elongate conidia with connectives visible between the conidia (UAMH 8920). Bar = 1 µm. **D**. Branching chain of asperulate conidia with scars (arrows) indicating position of side branches that have broken free (UAMH 8920). Bar = 1 µm.

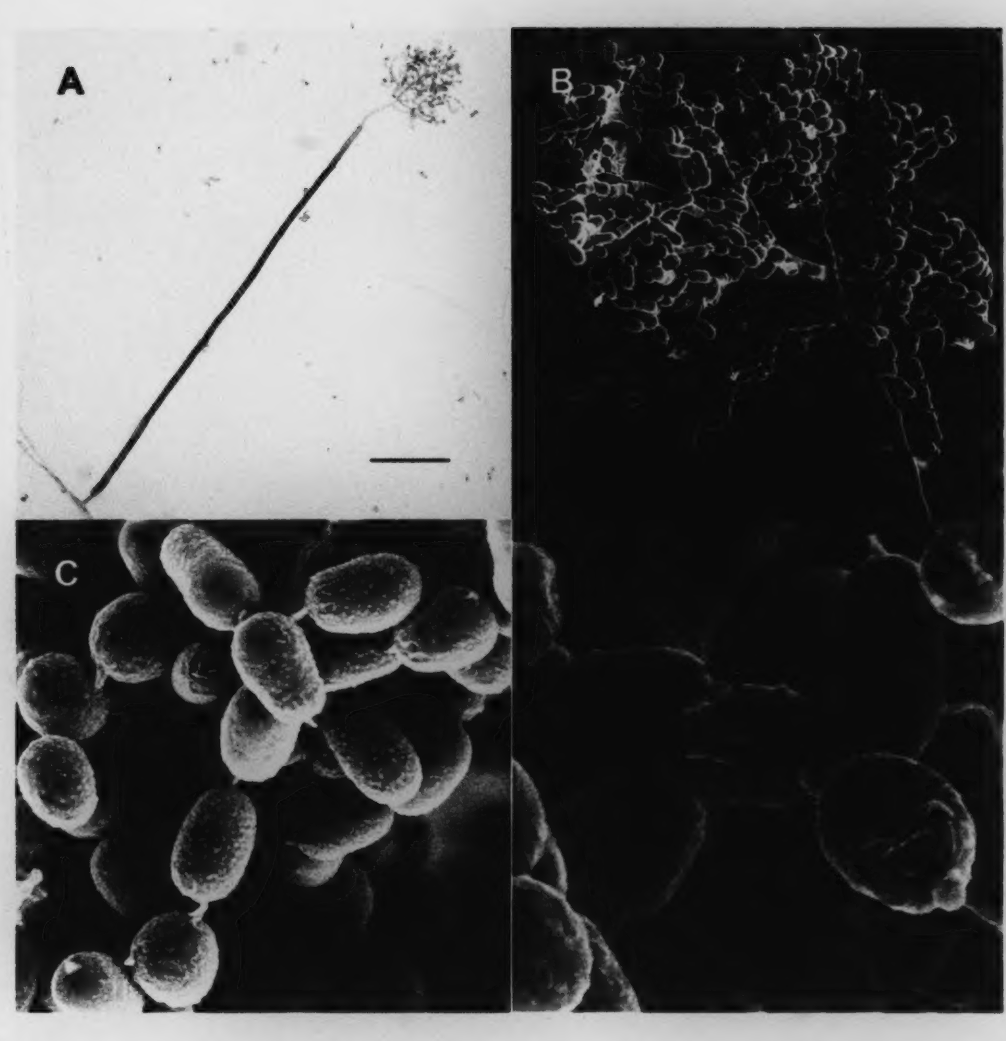

A
B
C

Figure 4.17. *Oidiodendron muniellense*. Reproduced with permission from Calduch *et al.* 2004 (Figures 2, 3, 6).

A. Conidiophores bearing straight, branched, melanized appendages and a conidial mass. Bar = 50 µm. **B**. Conidiophores bearing branched, melanized, fertile appendages. Bar = 40 µm. **C**. Globose to subglobose conidia with a reticulate network of spines. Bar = 5 µm.

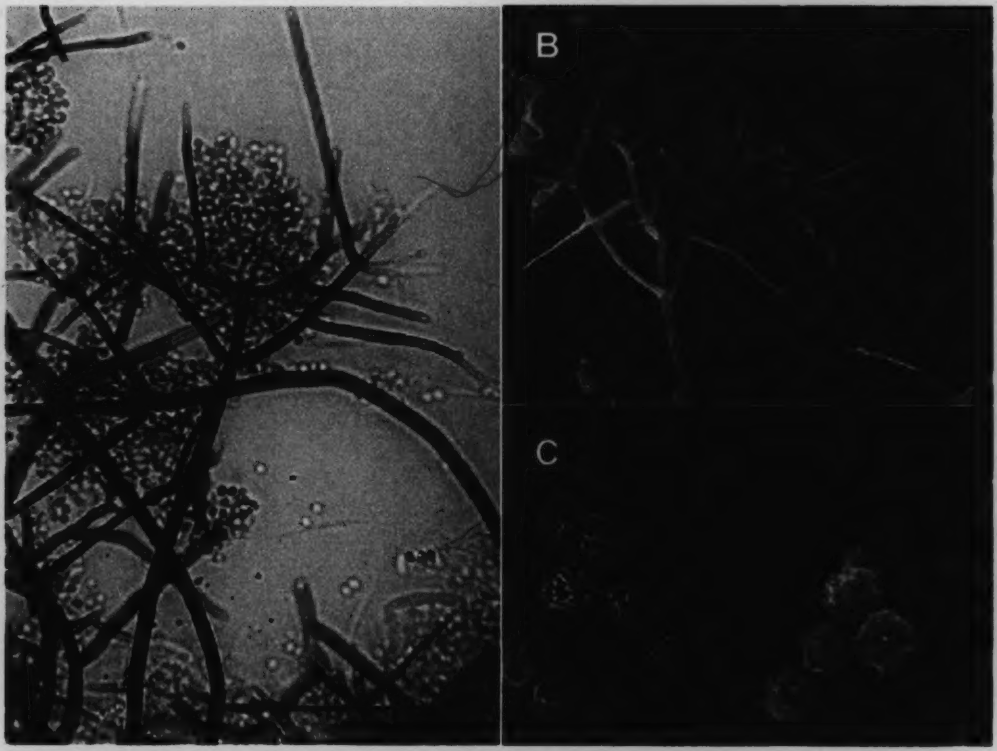

B
C

Figure 4.18. *Oidiodendron myxotrichoides*. Reproduced with permission from Calduch *et al.* 2002 (Figures 1, 10).

A. Sessile, reticuloperidium-like conidioma supporting fertile hyphae that fragment to produce ellipsoidal conidia. Bar = 50 µm. **B**. Ellipsoidal conidia with a rugose perispore with connectives visible between some of the conidia. Bar = 2 µm.

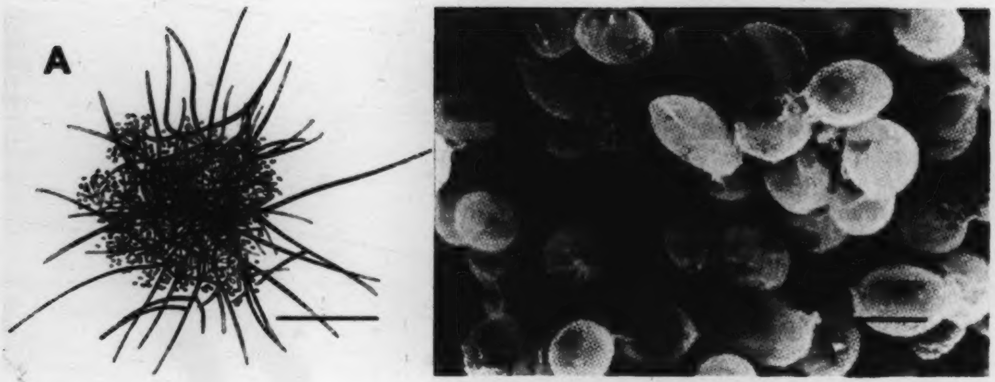

A

Figure 4.19. *Oidiodendron periconioides* (UAMH 8527).

A. Erect conidiophore bearing a dense head of dark, spinulose, subglobose to ellipsoidal conidia. Bar = 20 µm. **B**. Short chains of spinulose, subglobose to ellipsoidal conidia forming from swollen vesicles (arrows). Bar = 5 µm. **C**. Spinulose, globose to ellipsoidal conidia. Bar = 1 µm.

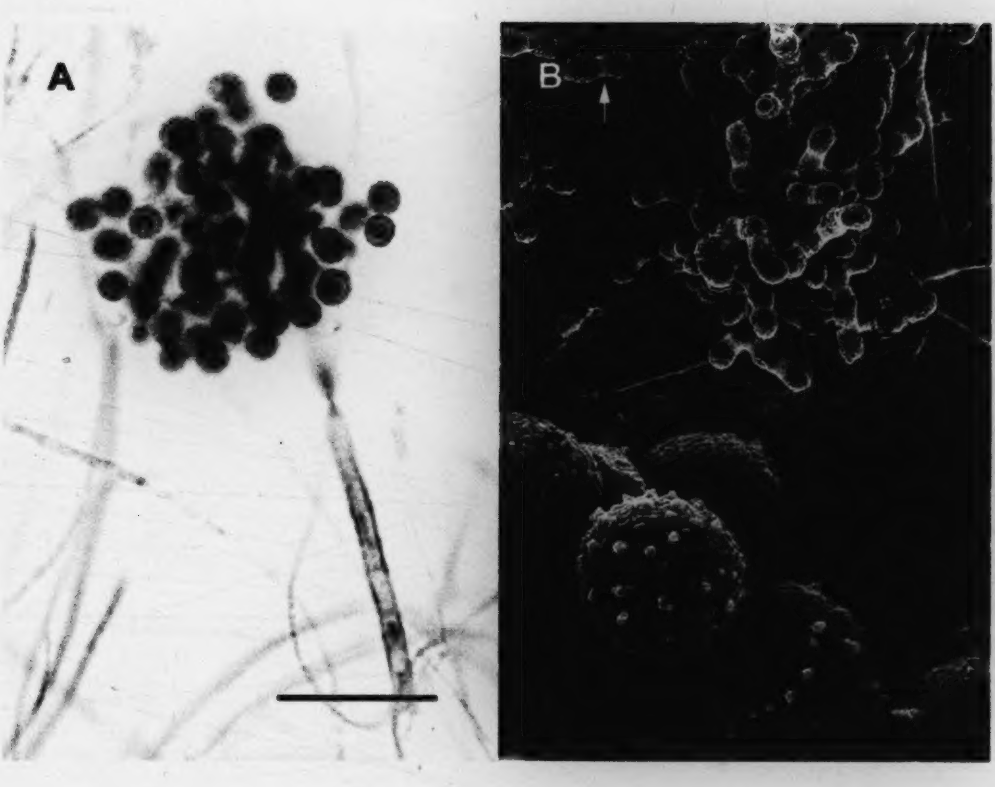

A
B

Figure 4.20. Tall conidiophore of *Oidiodendron pilicola* bearing oppositely branched, fertile hyphae that fragment to form branched chains of hyaline, smooth, barrel-shaped conidia with apical frills. Bar = 15 µm. Reconstructed from the description and illustrations provided by Kobayasi (1969).

4.20

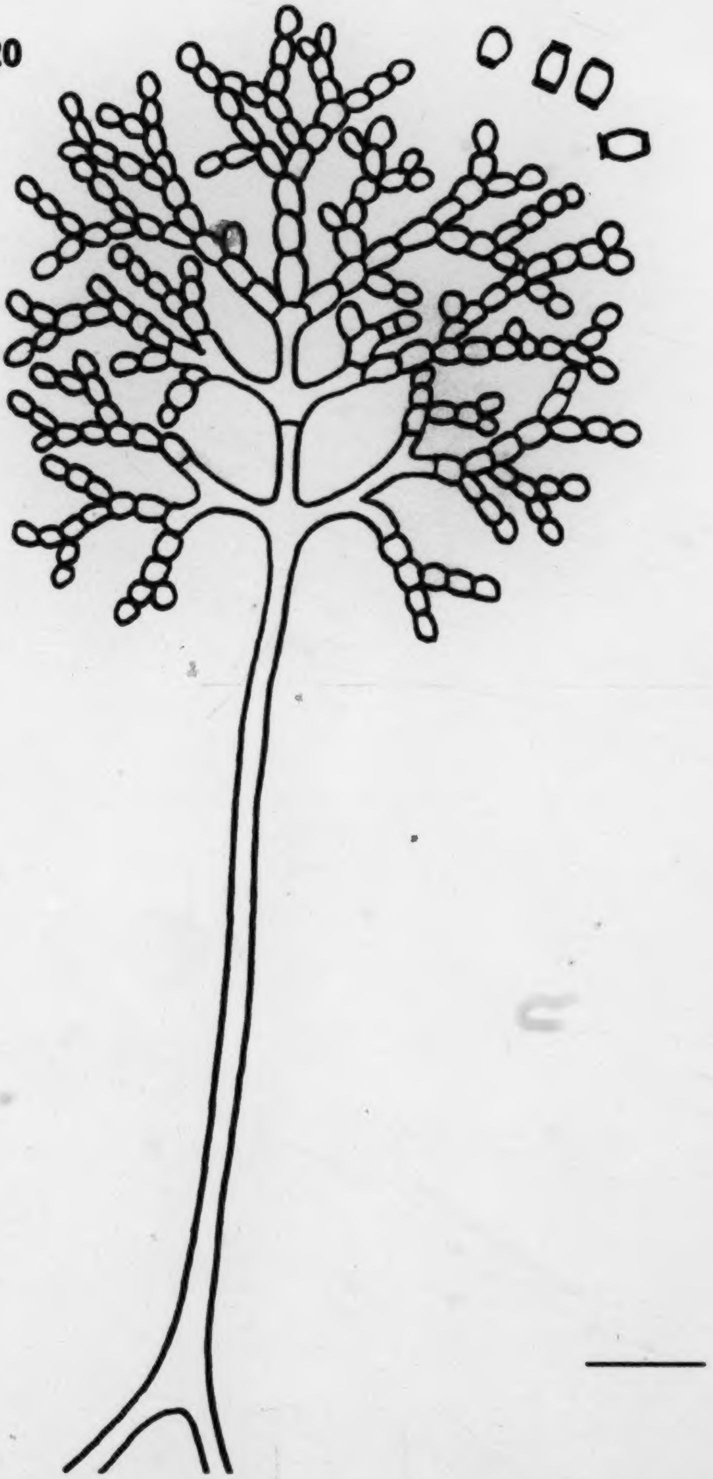


Figure 4.21. *Oidiodendron rhodogenum* (UAMH 1405).

A. Erect, dichotomously branched conidiophore bearing divergent, branched chains of thin-walled, subglobose to elongate or cylindrical conidia. Bar = 15 µm. **B**. Short chains of ellipsoidal to elongate conidia branching off of a portion of the conidiophore. Conidia have a rugose perispore. Bar = 5 µm. **C**. Chains of ellipsoidal to elongate or cylindrical conidia with a rugose perispore and connectives visible between conidia. Bar = 1 µm. **D**. Rugose, ellipsoidal to elongate conidia branching from a fertile hypha. Note scars left on conidia that have disarticulated. Bar = 1 µm.

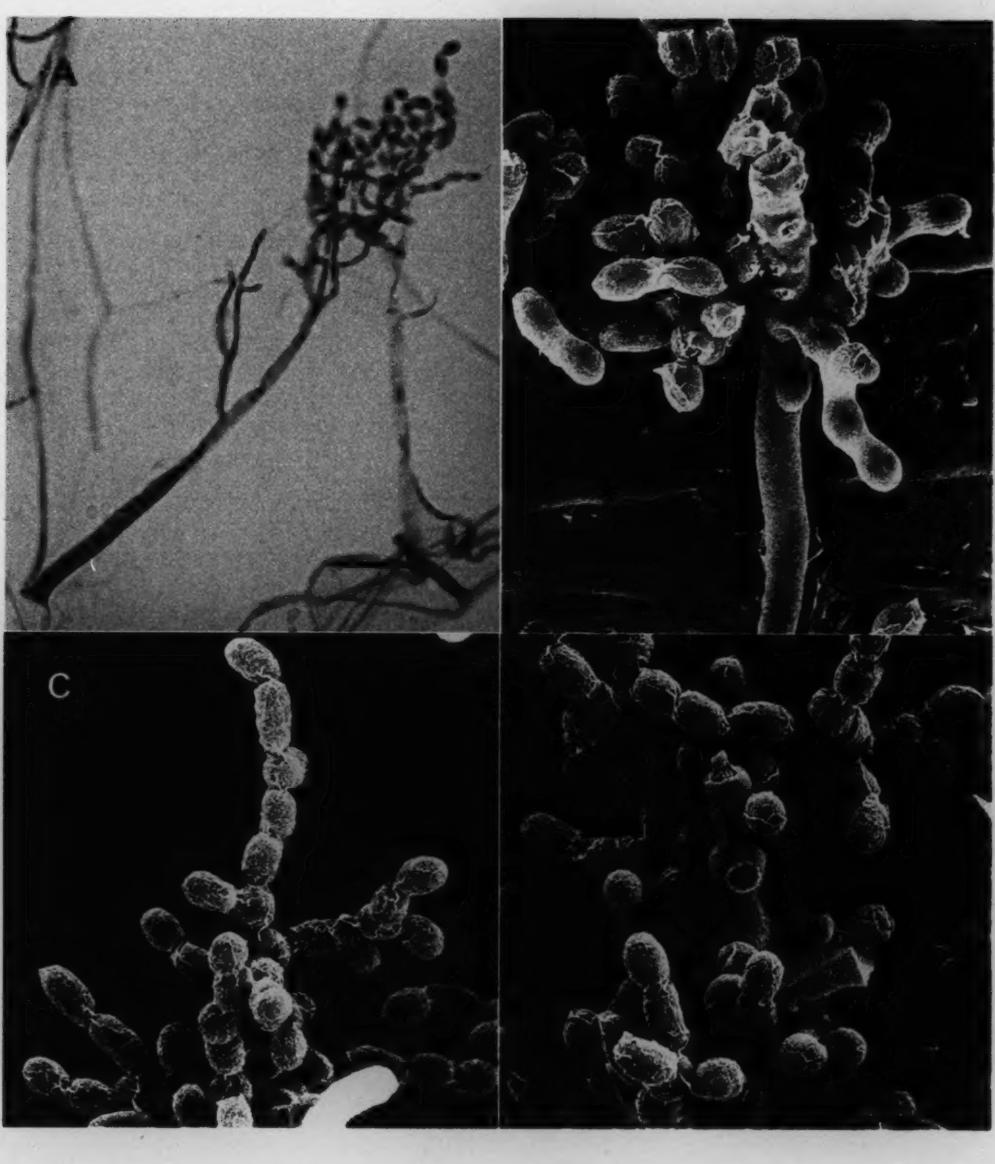

A
C

Figure 4.22. *Oidiodendron setiferum* (UAMH 5715) or reproduced with permission from Calduch *et al.* 2004 (Figures 12, 18).

A. Erect conidiophore bearing two dichotomously branched appendages and a dense head of thin-walled, hyaline to lightly pigmented, subglobose to elongate or irregular conidia (UAMH 5715). Bar = 15 µm. **B**. Conidiophores bearing long, branched, recurved appendages subtending central conidial masses (*O. ramosum*; Calduch *et al.* 2004, Figure 12). Bar = 100 µm. **C**. Apex of conidiophore bearing four dichotomously branched, recurved, fertile appendages and a small, central conidial mass. Arrows indicate fertile hyphae arising from the appendages (UAMH 5715). Bar = 10 µm. **D**. Fertile appendages with conidia arising from branching points and apices (UAMH 5715). Bar = 10 µm. **E**. Penicillate head of fertile hyphae fragmenting to form short chains of subglobose to ellipsoidal or elongate conidia with a rugose perispore. Connectives are visible between the conidia (UAMH 5715). Bar = 1 µm. **F**. Chains of subglobose to ellipsoidal conidia with a rugose perispore and a central dimple visible on some conidia (UAMH 5715). Bar = 1 µm. **G**. Subglobose to ellipsoidal conidia with a rugose perispore and a central dimple visible on some conidia (*O. ramosum*; Calduch *et al.* 2004, Figure 18). Bar = 1.75 µm.

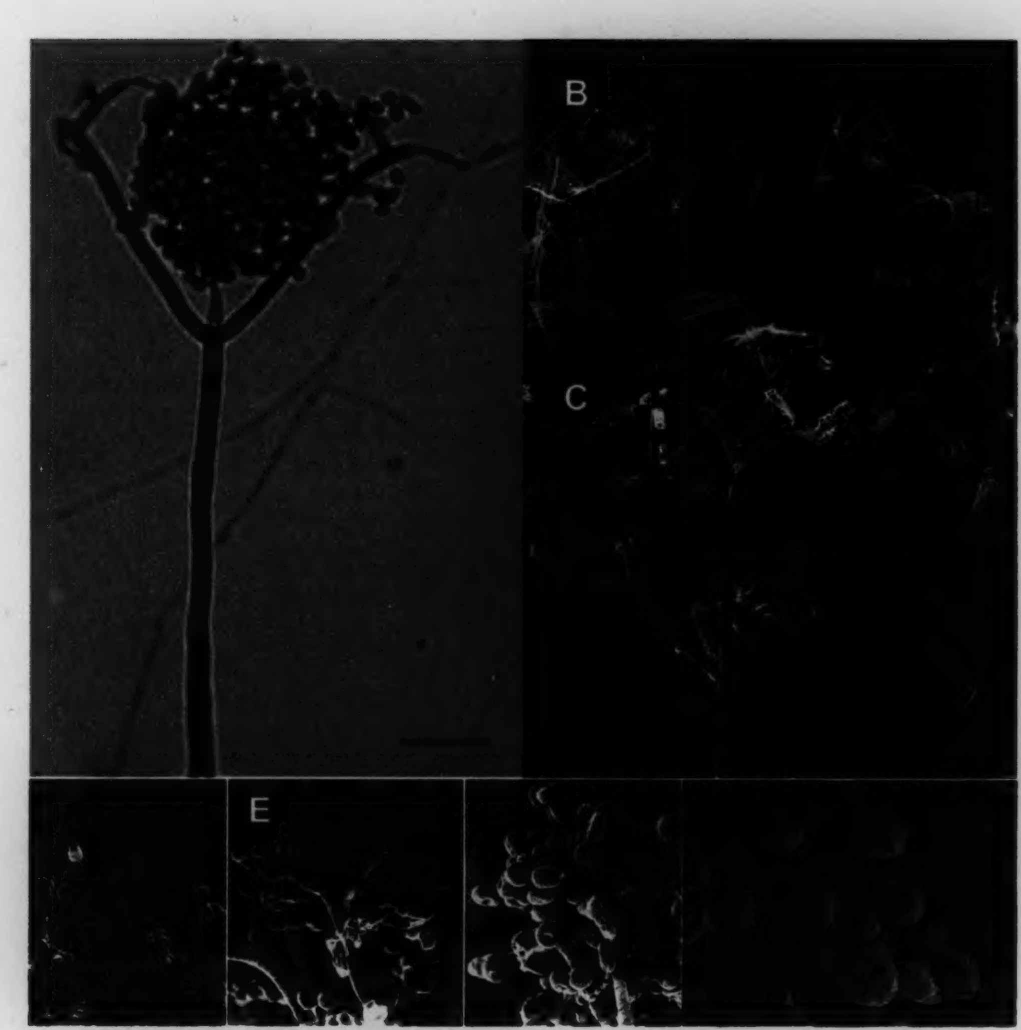

B
C
E

Figure 4.23. *Oidiodendron tenuissimum.*

A. Erect conidiophore bearing a dense head of thick-walled, dark, subglobose to elongate conidia (UAMH 8513). Bar = 15 µm. **B**. Short conidiophore bearing a large, dense head of long chains of spinulose, subglobose conidia (UAMH 8513). Bar = 10 µm. **C**. Spinulose, subglobose to ellipsoidal conidia of dried type material (NYS). Bar = 2 µm. **D**. Subglobose to ellipsoidal conidia with a network of spines (UAMH 8513). Bar = 1 µm.

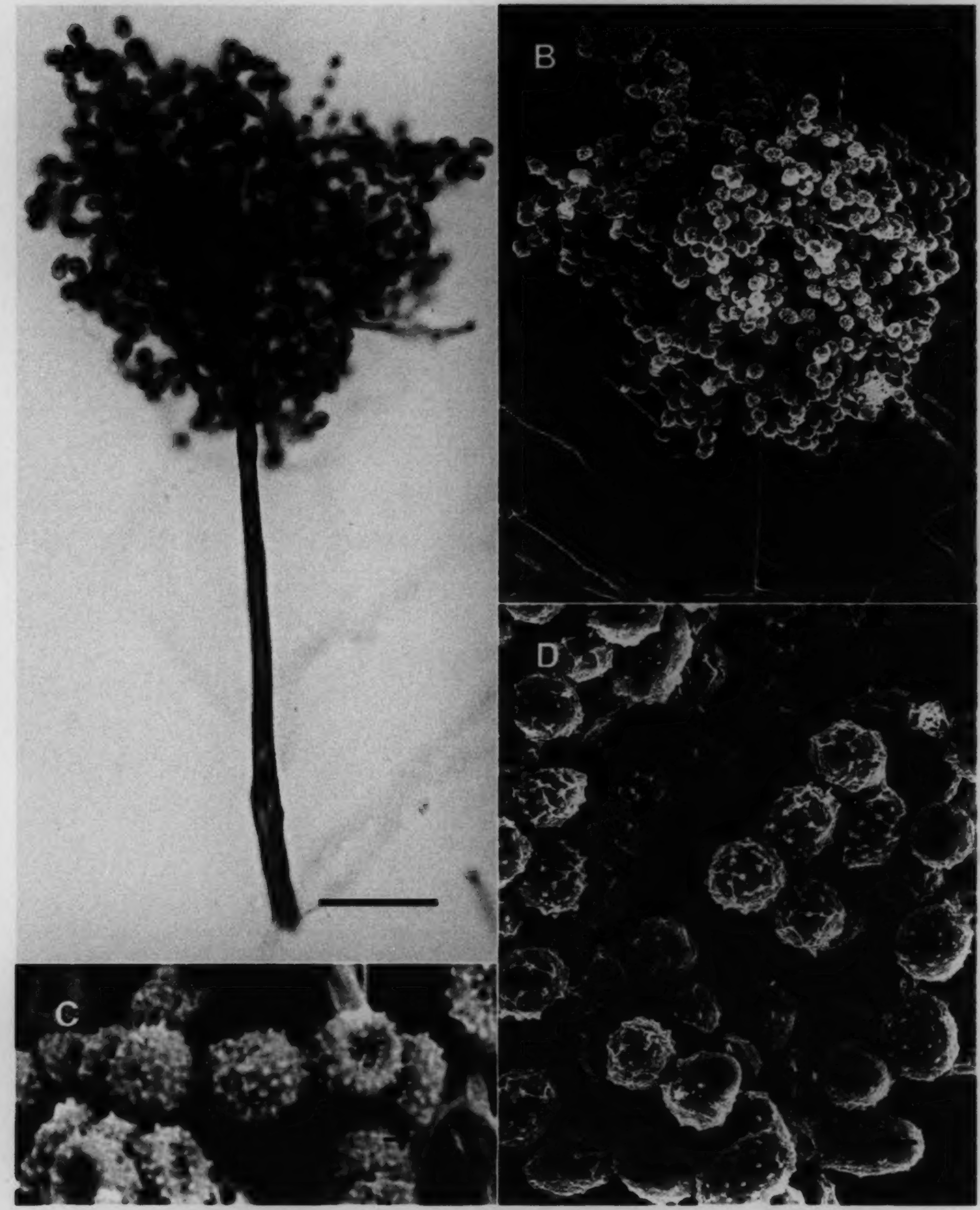
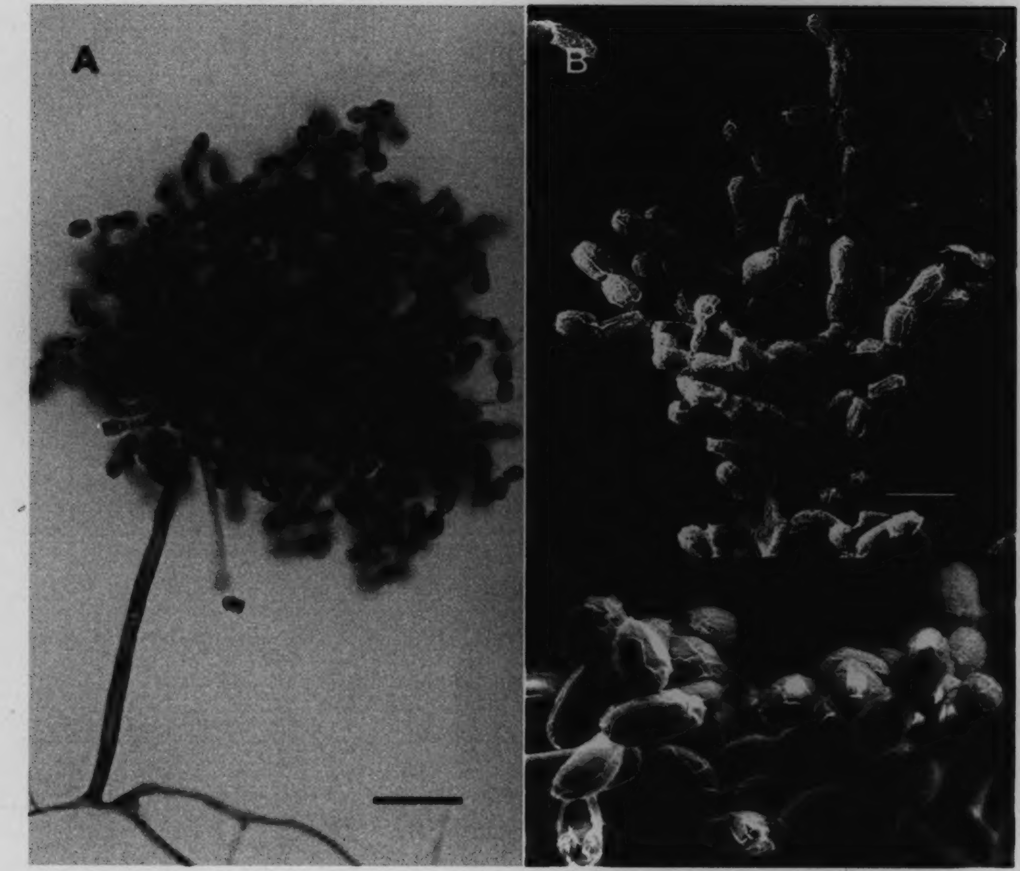

B
C
D

Figure 4.24. *Oidiodendron truncatum.*

A. Erect conidiophore bearing a large, dense head of thick-walled, truncate, dark, barrel-shaped conidia with apical frills (UAMH 1399). Bar = 15 µm. **B**. Branched chains of barrel-shaped conidia with a rugose (reticulate) perispore (UAMH 10464). Bar = 5 µm. **C**. Barrel-shaped conidia with a reticulate perispore (UAMH 10464). Bar = 1 µm.


A
B

4.7. Literature Cited

Barron GL (1962). New species and new records of *Oidiodendron. Canadian Journal of Botany* **40**: 589–607.

Barron GL, Booth C (1966). A new species of *Arachniotus* with an *Oidiodendron* conidial state. *Canadian Journal of Botany* **44**: 1057–1061.

Bending GD, Read DJ (1997). Lignin and soluble phenolic degradation by ectomycorrhizal and ericoid mycorrhizal fungi. *Mycological Research* **101**: 1348–1354.

Calduch M, Gené J, Cano J, Guarro J (2002). A new species of *Oidiodendron* with gymnothecium-like sporodochia. *Studies in Mycology* **47**: 211–216.

Calduch M, Gené J, Cano J, Stchigel A, Guarro J (2004). Three new species of *Oidiodendron* Robak from Spain. *Studies in Mycology* **50**: 159–170.

Couture M, Fortin JA, Dalpé Y (1983). *Oidiodendron griseum* Robak: an endophyte of ericoid mycorrhiza in *Vaccinium* spp. *New Phytologist* **95**: 375–380.

Currah RS (1985). Taxonomy of the *Onygenales*: *Arthrodermataceae, Gymnoascaceae, Myxotrichaceae* and *Onygenaceae*. *Mycotaxon* **24**: 1–216.

Currah RS (1994). Peridial morphology and evolution in the prototunicate ascomycetes. In: Hawksworth DL (ed) *Ascomycete Systematics: Problems and Perspectives in the Nineties*. Plenum Press, New York. pp 281–293.

Currah RS, Niemi M, Huhtinen S (1999). *Oidiodendron maius* and *Scytalidium vaccinii* from the mycorrhizas of *Ericaceae* in northern Finland. *Karstenia* **39**: 65–68.

Currah RS, Tsuneda A, Murakami S (1993). Conidiogenesis in *Oidiodendron periconioides* and ultrastructure of ericoid mycorrhizas formed with *Rhododendron brachycarpum*. *Canadian Journal of Botany* **71**: 1481–1485.

Dalpé Y (1986). Axenic synthesis of ericoid mycorrhiza in *Vaccinium angustifolium* Ait. by *Oidiodendron* species. *New Phytologist* **103**: 391–396.

Dalpé Y (1989). Ericoid mycorrhizal fungi in the *Myxotrichaceae* and *Gymnoascaceae*. *New Phytologist* **113**: 523–527.

Dalpé Y (1991). Statut endomycorrhizien du genre *Oidiodendron*. *Canadian Journal of Botany* **69**: 1712–1714.

Delamarre S, Batt CA (1999). The microbiology and historical safety of margarine. *Food Microbiology* **16**: 1712–1714.

Domsch KH, Gams W, Anderson T-H (1980). *Compendium of Soil Fungi*. Academic Press, United Kingdom.

Douglas GC, Heslin MC, Reid C (1989). Isolation of *Oidiodendron maius* from *Rhododendron* and ultrastructural characteristics of synthesized mycorrhizas. *Canadian Journal of Botany* **67**: 2206–2212.

Ellis MB (1971). *Dematiaceous Hyphomycetes*. Commonwealth Agricultural Bureaux, United Kingdom.

Ellis MB (1976). *More Dematiaceous Hyphomycetes*. Commonwealth Agricultural Bureaux, United Kingdom.

Gams W, Söderström BE (1983). *Oidiodendron scytaloides* n. sp. *Cryptogamie, Mycologie* **4**: 239–243.

Gibas CFC, Sigler L, Summerbell RC, Currah RS (2002). Phylogeny of the genus *Arachnomyces* and its anamorphs and the establishment of *Arachnomycetales*, a new eurotiomycete order in the *Ascomycota*. *Studies in Mycology* **47**: 131–139.

Greif MD, Currah RS (2003). A functional interpretation of the role of the reticuloperidium in whole-ascoma dispersal by arthropods. *Mycological Research* **107**: 77–81.

Hambleton S, Currah RS (1997). Fungal endophytes from the roots of alpine and boreal *Ericaceae*. *Canadian Journal of Botany* **75**: 1570–1581.

Hambleton S, Egger KN, Currah RS (1998). The genus *Oidiodendron*: species delimitation and phylogenetic relationships based on nuclear ribosomal DNA analysis. *Mycologia* **90**: 854–869.

Hawksworth DL (1974). *Mycologists Handbook*. Commonwealth Agricultural Bureaux, United Kingdom.

Hawksworth DL, Kirk PM, Sutton BC, Pegler DN (1995). *Ainsworth & Bisby's Dictionary of the Fungi*. 8th Edition. University Press, United Kingdom.

Horak B, Dutkiewicz J, Solarz K (1996). Microflora and acarofauna of bed dust from homes in Upper Silesia, Poland. *Annals of Allergy, Asthma, and Immunology* **76**: 41–50.

Hughes SJ (1958). Revisiones hyphomycetum aliquot cum appendice de nominibus rejiciendis. *Canadian Journal of Botany* **36**: 727–836.

Hutchison LJ (1990). Studies on the systematics of ectomycorrhizal fungi in axenic culture. II. The enzymatic degradation of selected carbon and nitrogen compounds. *Canadian Journal of Botany* **68**: 1522–1530.

Johansson M (2001). Fungal associations of Danish *Calluna vulgaris* roots with special reference to ericoid mycorrhiza. *Plant and Soil* **231**: 225–232.

Kobayasi Y (1969). Mycological flora of the Alaskan Arctic. *Bulletin of the National Science Museum (Tokyo)* **12**: 424–425.

Krysińska-Traczyk E, Kiecana I, Perkowski J, Dutkiewicz J (2001). Levels of fungi and mycotoxins in samples of grain and grain dust collected on farms in eastern Poland. *Annals of Agricultural and Environmental Medicine* **8**: 269–274.

Lacourt I, Girlanda M, Perotto S, Del Paro M, Zuccon D, Luppi AM (2001). Nuclear ribosomal sequence analysis of *Oidiodendron*: towards a redefinition of ecologically relevant species. *New Phytologist* **149**: 565–576.

Lumley TC, Gignac LD, Currah RS (2001). Microfungus communities of white spruce and trembling aspen logs at different stages of decay in disturbed and undisturbed sites in the boreal mixedwood region of Alberta. *Canadian Journal of Botany* **79**: 76–92.

Malan CE (1949). Su un nuovo reperto di *Dicyma ambigua* Peyronel e sulla posizione sistematica di questa specie. *Giornale Botanico Italiano* **56**: 735–738.

Melin E, Nannfeldt JA (1934). Researches into the bluing of ground woodpulp. *Saertryck ur Svenska Skogsvårdsföreningens Tidskrift Hafte* **3-4**: 397–616.

Mercado Sierra A, Casteñeda Ruiz RF (1985). Nuevos hifomicetes tálicos de Cuba. *Acta Botanica Cubana* **32**: 1–10.

Miyamoto T, Igarashi T, Takahashi K (2000). Lignin-degrading activity of litter-decomposing basidiomycetes from *Picea* forests of Hokkaido. *Mycoscience* **41**: 105–110.

Mori Y, Sato Y, Takamatsu S (2000). Molecular phylogeny and radiation time of *Erysiphales* inferred from the nuclear ribosomal DNA sequences. *Mycoscience* **41**: 437–447.

Morrall RAA (1968). Two new species of *Oidiodendron* from boreal forest soils. *Canadian Journal of Botany* **46**: 203–206.

Orr GF, Kuehn HH (1964). A re-evaluation of *Myxotrichum spinosum* and *Myxotrichum cancellatum*. *Mycologia* **56**: 473–481.

Orr GF, Kuehn HH, Plunkett OA (1963). The genus *Myxotrichum* Kunze. *Canadian Journal of Botany* **41**: 1457–1480.

Perotto S, Perotto R, Faccio A, Schubert A, Varma A, Bonfante P (1995). Ericoid mycorrhizal fungi: cellular and molecular bases of their interactions with the host plant. *Canadian Journal of Botany* **73**: S557–S568.

Peyronel B (1914). Osservazioni critiche e sperimentali su alcune specie del genere *Dicyma* Boul. e sui loro stati ascofori. *Annales Mycologici* **12**: 459–470.

Piercey MM, Thormann MN, Currah RS (2002). Saprobic characteristics of three fungal taxa from ericalean roots and their association with the roots of *Rhododendron groenlandicum* and *Picea mariana* in culture. *Mycorrhiza* **12**: 175–180.

Pivkin MV (2000). Filamentous fungi associated with Holothurians from the Sea of Japan, off the Primorye Coast of Russia. *Biological Bulletin* **198**: 101–109.

Reiman M, Uitti J (2000). Exposure to microbes, endotoxins, and total dust in cigarette and cigar manufacturing: an evaluation of health hazards. *Annals of Occupational Hygeine* **44**: 467–473.

Rice AV, Currah RS (2001). Physiological and morphological variation in *Oidiodendron maius*. *Mycotaxon* **79**: 383–396.

Rice AV, Currah RS (2002). New perspectives on the niche and holomorph of the myxotrichoid hyphomycete, *Oidiodendron maius*. *Mycological Research* **106**: 1463–1467.

Rice AV, Currah RS (in press 1). Profiles from Biolog FF plates and morphological characteristics support the recognition of *Oidiodendron fimicolum* sp. nov. *Studies in Mycology* (accepted March 2005).

Rice AV, Currah RS (in press 2). *Oidiodendron maius*: Saprobe in *Sphagnum* peat, mutualist in ericaceous roots? In: Schulz B, Boyle C, Sieber T (eds) *Microbial Root Endophytes*. Springer-Verlag, Heidelberg (Accepted Jan. 2005).

Robak H (1932). Investigations regarding fungi on Norwegian ground woodpulp and fungal infections at woodpulp mills. *Saertrykk av Nyt Magazin for Naturvidenskaberne* **71**: 185–330.

Roose-Amsaleg C, Brygoo Y, Harry M (2004). Ascomycete diversity in soil-feeding termite nests and soils from a tropical rainforest. *Environmental Microbiology* **6**: 462–469.

Roy RY, Singh GN (1969). A new species of *Oidiodendron* from Indian soil. *Journal of the Indian Botanical Society* **48**: 159–160.

Sigler L, Carmichael JW (1976). Taxonomy of *Malbranchea* and some other hyphomycetes with arthroconidia. *Mycotaxon* **4**: 349–488.

Sigler L, Flis A (1998). *Catalogue of the University of Alberta Microfungus Collections and Herbarium*, 3rd Edition. University of Alberta, Edmonton, AB, Canada. (available online at www.devonian.ualberta.ca/uamh)

Sigler L, Gibas CFC (in press). Utility of a cultural method for identification of the ericoid mycobiont *Oidiodendron maius*. *Studies in Mycology* (accepted 2004).

Sigler L, Lumley TC, Currah RS (2000). New species and new records of saprophytic ascomycetes (*Myxotrichaceae*) from decaying logs in the boreal forest. *Mycoscience* **41**: 495–502.

Smith G (1946). Note on the occurrence of species of *Oidiodendron* Robak in Britain. *British Mycological Society Transactions* **29**: 232–234.

Smith RE (1977). Rapid tube test for detecting fungal cellulase production. *Applied Environmental Microbiology* **33**: 980–981.

Söderström BE, Bååth E (1978). Soil microfungi in three Swedish coniferous forests. *Holarctic Ecology* **1**: 62–72.

Stalpers J (1974). Revision of the genus *Oedocephalum* (Fungi Imperfecti). *Koninklijk Nederlandse Akademie van Wetenschappen – Amsterdam*. **77**: 383–402.

Sugiyama S, Ohara A, Mikawa T (1999). Molecular phylogeny of onygenalean fungi based on small subunit ribosomal DNA (SSU rDNA) sequences. *Mycoscience* **40**: 251–258.

Tewari RP, MacPherson CR (1968). Pathogenicity and neurologic effects of *Oidiodendron kalrai* for mice. *Journal of Bacteriology* **95**: 1130–1139.

Tewari RP, MacPherson CR (1971). A new dimorphic fungus, *Oidiodendron kalrai*: morphological and biochemical characteristics. *Mycologia* **63**: 602–611.

Thormann MN, Currah RS, Bayley SE (2001). Microfungi isolated from *Sphagnum fuscum* from a southern boreal bog in Alberta. *The Bryologist* **104**: 548–559.

Tokumasu S (1973). Notes on Japanese *Oidiodendron*. *Transactions of the Mycological Society of Japan* **14**: 246–255.

Tribe HT, Weber RWS (2002). A low-temperature fungus from cardboard, *Myxotrichum chartarum*. *Mycologist* **16**: 3–5.

Tsuneda A, Currah RS (2004). Ascomatal morphogenesis in *Myxotrichum arcticum* supports the derivation of the *Myxotrichaceae* from a discomycetous ancestor. *Mycologia* **96**: 627–635.

Tsuneda A, Thormann MN, Currah RS (2001). Modes of cell wall degradation of *Sphagnum fuscum* by *Acremonium* cf. *curvulum* and *Oidiodendron maius*. *Canadian Journal of Botany* **79**: 93–100.

Uchiyama S, Kamiya S, Udagawa S (1995). Five onygenalean fungi from Japan. *Mycoscience* **36**: 211–220.

Udagawa S, Toyazaki N (1987). A new species of *Oidiodendron*. *Mycotaxon* **28**: 233–240.

Udagawa S, Uchiyama S (1998). Three hyphomycetes isolated from soil and feather debris. *Canadian Journal of Botany* **76**: 1637–1646.

Udagawa S, Uchiyama S (1999). Taxonomic studies on new or critical fungi of non-pathogenic *Onygenales* 1. *Mycoscience* **40**: 277–290.

Udagawa S, Uchiyama S (2000). Two onygenalean fungi from Russian Far East soil. *Mycoscience* **41**: 217–221.

Udagawa S, Uchiyama S, Kamiya S (1993). *Gymnostellatospora*, a new genus of the *Myxotrichaceae*. *Mycotaxon* **48**: 157–164.

Udagawa S, Uchiyama S, Kamiya S (1994). A new species of *Myxotrichum* with an *Oidiodendron* anamorph. *Mycotaxon* **52**: 197–205.

Usuki F, Abe JP, Kakishima M (2003). Diversity of ericoid mycorrhizal fungi isolated from hair roots of *Rhododendron obtusum* var. *kaempferi* in a Japanese red pine forest. *Mycoscience* **44**: 97–102.

Von Szilvinyi A (1941). Mikrobiologische Boden untersuchungen im Lunzer Bebiet. *Zentralblatt für Bakteriologie Abietlung II*. **103**: 133–189.

Xiao G, Berch S (1999). Organic nitrogen use by salal ericoid mycorrhizal fungi from northern Vancouver Island and impacts on growth *in vitro* of *Gaultheria shallon*. *Mycorrhiza* **9**: 145–149.

Zhadanova NN (1963). Redki ta novi vydy temnozabarvlenykh hifomitsetiv v hruntakh Ukranyiny. (Rare and new species of dark-coloured hyphomycetes in the soils of the Ukraine). *Mikrobiologiecheskiy Zhurnal Akademiya Nauk Unkrainskiy RSR*. **25**: 13–19.

CHAPTER 5: TWO NEW SPECIES OF *PSEUDOGYMNOASCUS* WITH *GEOMYCES* ANAMORPHS AND THEIR PHYLOGENETIC RELATIONSHIP WITH *GYMNOSTELLATOSPORA*[4]

5.1. Introduction

Pseudogymnoascus Raillo was included in the *Myxotrichaceae* (*Ascomycota*) (Currah 1985) based on the production of ellipsoidal to fusoid, single-celled, hyaline ascospores in globose, evanescent asci, its distinctive yellow to reddish gymnothecial ascomata and cellulolytic abilities. *Pseudogymnoascus roseus* Raillo is the type of the genus (Currah 1985) and appears regularly in surveys of fungi associated with soil (e.g. Raillo 1929, Cejp & Milko 1966, Samson 1972, Currah 1985), roots (Currah 1985), and wood (Sigler *et al.* 2000, Lumley *et al.* 2001). *Pseudogymnoascus roseus* var. *ornatus* Udagawa & Uchiyama is the only other taxon in the genus (Udagawa & Uchiyama 1999) and is distinguished from the type variety in having lobate reticulate rather than smooth ascospores. Both varieties have dendritic arthroconidial anamorphs in the genus *Geomyces* Traaen. Within the *Myxotrichaceae*, the genus *Gymnostellatospora* Udagawa, Uchiyama & Kamiya is most similar to *Pseudogymnoascus* in having lightly coloured ascomata but is distinctive in producing ascospores with prominent longitudinal ridges. *Geomyces* anamorphs have been reported, but not confirmed, for at least one *Gymnostellatospora* species [*Gy. dendroidea* (Locquin-Linard) Udagawa] (Sigler *et al.* 2000). *Myxotrichum* Kunze, along with a range of affiliated *Oidiodendron* Robak species and anamorphs (Hambleton *et al.* 1998, Rice & Currah, in press), is distinguished from *Pseudogymnoascus*, *Gymnostellatospora*, and affiliated *Geomyces* species by having deeply melanized hyphae associated with sporulating structures (peridial hyphae and conidiophores) (Currah 1985, Sigler *et al.* 2000).

The *Myxotrichaceae* was originally placed in the *Onygenales* with other cleistothecial ascomycetes that have arthroconidial anamorphs (Currah 1985). However, molecular evidence suggests that the *Myxotrichaceae* is affiliated with the inoperculate discomycetes (*Leotiomycetes*) rather than the *Onygenales* (Sugiyama *et al.* 1999, Mori *et al.* 2000, Gibas *et al.* 2002). DNA sequence data also suggest that *Myxotrichum* and *Oidiodendron* form a separate lineage from *Pseudogymnoascus*, *Gymnostellatospora*, and *Geomyces* (Mori *et al.* 2000, Gibas *et al.* 2002).

During a survey of cellulose- and lignin-degrading fungi in a *Sphagnum* bog in the southern boreal forest of western Canada, I obtained numerous isolates of *Geomyces* species from bait blocks made of brown-rotted spruce wood which had been set into the upper layers of the *Sphagnum* moss for eight to twelve months. Some of these isolates developed ascomata similar to those found in *Pseudogymnoascus* and *Gymnostellatospora* but their characteristics did not match any of the described species.

---

[4] A version of this chapter has been submitted for publication: Rice AV, Currah RS (submitted) Two new species of *Pseudogymnoascus* with *Geomyces* anamorphs and their phylogenetic relationship with *Gymnostellatospora*. *Mycologia* (submitted July 2005).

Two new species were discerned: one with smooth, orange peridial hyphae, long, branched appendages, and ascospores with a faint longitudinal rim, and another with warty, red to red-brown peridial hyphae, short, unbranched appendages, irregularly ornamented ascospores, and smooth to asperulate and irregularly warty conidia. Because these suites of characters suggested the new species might occupy intermediate positions between *Pseudogymnoascus* and *Gymnostellatospora*, I compared the nuclear ribosomal DNA (rDNA) region consisting of the Internal Transcribed Spacer (ITS) regions 1 and 2 and the 5.8S gene of 24 isolates, representing the two new species and 11 similar anamorphic or teleomorphic taxa in the *Myxotrichaceae*.

5.2. Materials and Methods

Cultures and holotype specimens of *Pseudogymnoascus appendiculatus* nom. prov. and *P. verrucosus* nom. prov. are deposited at the University of Alberta Microfungus Collection and Herbarium (UAMH). Cultures for sequencing were obtained from UAMH (Table 5.1). Living cultures of *P. roseus* var. *ornatus*, *Gymnostellatospora parvula* Udagawa & Uchiyama, and *Gy. dendroidea* are not available from culture collections. A sequence for *Myxotrichum chartarum* Kunze was obtained from GenBank.

5.2.1. Isolation and Description of the New Species

Ascomata were produced in several cultures of strains identified as *Geomyces* spp. after several-months incubation at 5 and 15°C. Single ascospore isolates were plated onto cornmeal agar [CMA; 17 g BBL cornmeal agar (Becton Dickinson Co., Sparks, MD), 1 l dH_2O] and oatmeal agar [OA; 20 g ground Quaker oatmeal cereal, 20 g BBL agar (Becton Dickinson Co.), 1 l dH_2O] and incubated at 5 and 15°C. Cultures were described on CMA and OA and the ascomata and ascospores were examined using light and scanning electron microscopy. Ascomata were mounted in polyvinyl alcohol mounting media [PVA; 16.6 g polyvinyl alcohol (Sigma Chemical Co., St. Louis, MO), 100 ml dH_2O, 100 ml lactic acid (Fisher Scientific, Fair Lawn, NJ), 10 ml glycerin (Fisher Scientific)] and PVA with acid fuschin (APVA; Sigma), examined using an Olympus BX50 light microscope (Olympus Optical Co., Tokyo, Japan), and photographed using an Olympus DP-12 digital camera (Olympus Optical Co.). Agar plugs with ascomata were prepared for scanning electron microscopy (SEM) using air drying, osmium fixation and critical point drying (Tsuneda *et al.* 2001), or freeze drying in liquid nitrogen and viewed under a Hitachi S-510 (Hitachi Science Systems, Japan) or a JEOL #JSM-6301FX7V (JEOL USA Inc., Peabody, MA) field emission SEM.

5.2.2. DNA Sequencing

Three isolates of *P. appendiculatus* and two of *P. verrucosus* were sequenced. Isolates of *Geomyces asperulatus* Sigler & Carmichael (UAMH 183, 9032), *G. pannorum* (Link) Sigler & Carmichael (UAMH 714, 1030, 1088), *Geomyces* sp. (UAMH 7253, 9107), *Gymnostellatospora alpina* (Müller & von Arx) Udagawa (UAMH 9339, 9430), *Gy. canadensis* Lumley, Sigler & Currah (UAMH 8899, 9238), *Gy. frigida* Uchiyama, Kamiya & Udagawa (UAMH 9304), *Gy. japonica* Udagawa (UAMH 9239, 9240), *Gy. subnuda* Sigler, Lumley & Currah (UAMH 9242), and *P. roseus* (UAMH 1653, 2879, 9163, 9222) were obtained from UAMH and were newly sequenced (Table 5.1). For outgroup comparison, a sequence of *Myxotrichum chartarum* (AF062813) was obtained from GenBank.

Cultures were grown on OA overlaid with a cellophane membrane (Carmichael 1962, Gibas *et al.* 2002). DNA extraction followed a modification of Cubero *et al.* (1999) and Gibas *et al.* (2002). Approximately 100 mg of mycelium was scraped from the surface of the cellophane membrane and placed in a sterile 2 ml screw-cap microcentrifuge tube, containing acid-washed sand, a ceramic bead, and 750 µl CTAB extraction buffer (2% w/v cetyl-trimethyl ammonium bromide, 1 M NaCl, 100 mM Tris, 20 mM EDTA). The mycelium was ground by centrifuging for at least 2 min at maximum speed. The mixture was transferred to a second tube and 1.5 µl B-mercaptoethanol was added before incubating for 2 hours at 65°C. Seven hundred fifty µl of chloroform:isoamyl alcohol (24:1 v/v) was added and the solution was mixed by inverting the tube about 20 times and centrifuging for 15 min at 10000 x g at room temperature. The upper aqueous layer, containing crude DNA, was collected and purified using the QIAquick PCR purification kit (QIAGEN Inc., Mississauga, ON). Purified DNA was stored at –20°C.

The nuclear rDNA region that includes ITS 1, 5.8S, and ITS 2, was amplified using the primer pair NS1/ITS4 (White *et al.* 1990). PCR reactions were subjected to 30 cycles on a Perkin Elmer GeneAmp 9700 Thermal Cycler (PE Applied Biosystems, Foster, CA). Both strands were sequenced with primers ITS1, ITS2, ITS3, and ITS4 using the BigDye™ Terminator Cycle Sequencing Kit (Applied Biosystems) and run on an ABI 377 Automated Sequencer (Amersham Pharmacia Biotech Inc, Piscataway, NJ). Consensus sequences were obtained using Sequencher™ 4.0.2 (Gene Codes Corp., Ann Arbor, MI) and aligned manually by eye using SeAl v. 2.0.a11 (University of Oxford, UK). Phylogenetic analyses were run using PAUP

(Phylogenetic Analysis Using Parsimony) v. 4.0b 10 (Swofford 2002) and the robustness of the resulting phylogenetic trees and inferred clades was tested using bootstrap analysis (Felsenstein 1985) of 100 resamplings.

5.3. Results

5.3.1. Taxonomy

Pseudogymnoascus appendiculatus Rice and Currah **nom. prov.** Figures 5.1, 5.2.

Etym.: Latin, *appendiculatus* = appendage, referring to the prominent, long, branched appendages.

Ascomata fiunt in frigore 2-8 menses post incubationem, vel solitaria vel in globis, globosa ad subglobosa, primum alba, deinde aurantiaco-brunnea in maturitate, appendicibus inclusis 300-650 μm diam. Hyphae peridiales aurantiaco-flavae, leves, septatae, crassiter tunicatae, 2-2.5μ m diam, ramosae, anastomosis reticuloperidium format. Appendices aurantiaco-flavae, crassiter tunicatae, septatae, dichotomose ramosae, leves, cum extremis fastigatis, 40-120 μm longae. Asci octospori, hyalini, globosi ad subglobosi, deliquescentes, 5-7 μm diam. Ascosporae 2.5-5 x 1.5-2.5 μm, hyalinae, fusoideae ad ellipsoideae, crista longitudinalis et indistincta. Status anamorphosis a Geomyci. Conidiophora tenuiter distincta, erecta, hyalina, tenuiter et leviter tunicata, dendritica, verticillate ramosa. Conidia alba ad pallide alba. Conidia terminalia subglobosa ad late pyriformia, cicatrix basalis et prominens, levia ad minute asperulata, 2.5-3.5 x 1.5-2.5 μm. Conidia intercalaria subglobosa ad elongata et dolioformia, extremis vel magis vel minus truncatis, levia ad minute asperulata, 3-5 x 2-2.5 μm. Isolata ex ligno brunneo-putrefacto piceae marianae in sphagno palustro submersae.

Holotypus: Colonia exsiccata ex UAMH 10509 *isolato ex ligno brunneo-putrefacto piceae marianae in sphagno palustro submersae.*

Colonies on OA 40-45 mm diam at 28 days at 15 °C and 38-47 mm diam at 5 °C, appressed, white, producing a diffusible yellow pigment and a clear exudate; reverse yellow. Aerial conidia abundant, white. Colonies on CMA 35-40 mm diam. at 15 °C and 33-40 mm diam at 5 °C, appressed, colourless, consisting of immersed, hyaline hyphae; reverse colourless. Aerial conidia sparse, patchy, white. Ascomata produced after 2-8 months on CMA at 5 °C and 15 °C and after 3 months on OA at 5°C. Ascomata solitary or clumped, globose to subglobose, white when immature, peridial hyphae and appendages darkening to orange-brown at maturity (Figure 5.1A), 200-450 μm diam excluding appendages, 300-650 μm diam including appendages (Figures 5.1A, 5.2A); centrum white at maturity. Peridial hyphae orange, smooth, septate, thick-walled, 2-2.5

µm diam, branched and anastomosing to form a reticuloperidium, giving rise to appendages (Figures 5.1B, 5.2B). Appendages orange, thick walled, septate, thickened at septa, branched, smooth, with tapered ends, 40-120 µm long (Figures 5.1B, 5.2B). Asci 8-spored, hyaline, globose to subglobose at maturity, deliquescent, 5-7 µm diam (Figures 5.1C, 5.2E). Immature asci subglobose to globose (Figure 5.2D,E) or clavate (Figure 5.2C), stipitate and borne singly (Figure 5.2C,E), or sessile and borne in chains (Figure 5.2D). Ascospores hyaline, fusoid to ellipsoidal, thick-walled, smooth or with an indistinct longitudinal rim, 2.5-5 x 1.5-2.5 µm (Figures 5.1D, 5.2F,G). Anamorph: *Geomyces* sp. (Figures 5.1E-G, 5.2H,I). Conidia produced on solitary, verticillately branched conidiophores (Figure 5.1E), in long chains on undifferentiated hyphae (Figure 5.1F), or on synnematous bundles of conidiophores (Figures 5.1G, 5.2I). Conidiophores erect, hyaline, thin- and smooth- walled, dendritic with verticillate branching, 5-40 x 1.5-2.5 µm, branches fragmenting basipetally into rhexolytically dehiscent arthroconidia and aleurioconidia. Conidia white to off-white *en masse*. Aleurioconidia terminal, subglobose to broadly pyriform with prominent truncate basal scars, hyaline, relatively thin-walled, smooth to minutely asperulate, 2.5-3.5 x 1.5-2.5 µm. Intercalary arthroconidia subglobose to elongate and barrel-shaped with more or less truncate ends, hyaline, thin-walled, smooth to minutely asperulate, 3-5 x 2-2.5 µm.

Holotype: Dried culture of isolate UAMH 10509 from brown-rotted black spruce wood buried under *Sphagnum* peat. Holotype and *ex*-type are deposited as UAMH 10509.

Other material: **Canada**. Alberta: 5 km east of Perryvale (54° 28' N, 113° 16' W), *Picea mariana-Sphagnum fuscum* bog, *ex* brown-rotted wood bait blocks, 2002, A. Rice (UAMH 10510, UAMH 10511, UAMH 10512)

Pseudogymnoascus verrucosus Rice and Currah **nom. prov**. Figures 5.3, 5.4.

Etymology: Latin, *verrucosus*=covered with warts, referring to the warty ornamentation of the peridial appendages, ascospores, and conidia.

Ascomata fiunt in frigore post 6-8 menses, vel solitaria vel in globis, globosa ad subglobosa, primum alba, deinde rubra in maturitate, 150-400 µm diam. Hyphae peridiales rubro-brunneae, septatae, crassiter tunicatae, 2-2.5 µm diam, crassiter asperulatae, alte ramosae; anastomosis reticuloperidium densum format. Appendices elongatae absunt, hyphae peridiales terminant in appendicibus nonnullis et distinctis, tumidis, subhyalinis, verrucosis, 5-10 x 3-4 µm. Asci octospori, hyalini, globosi ad subglobosi, deliquescentes, 5-8 µm diam. Ascosporae 3-5 x 2-3 µm, late fusoideae ad ellipsoideae, hylinae, perispora irregulariter asperulata ad verrucosa. Status anamorphosis a Geomyci. Conidiophora tenuiter distincta, erecta, hyalina, tenuiter et leviter *tunicata, dendritica, verticillate ramosa. Conidia alba, massiter ad pallide rosea. Conidia terminalia subglobosa ad late pyriformia, cicatrix basalis et prominens, asperulata ad irregulariter verrucosa in maturitate, 2.5-4 x 2-3 µm. Conidia intercalaria subglobosa ad elongata et dolioformia, extremis vel magis vel minus truncatis, asperulata ad irregulariter verrucosa, 2.5-5 x 2-3 µm. Isolata ex ligno brunneo-putrefacto piceae marianae in sphagno palustro submersae.*

Holotypus: Colonia exsiccata ex UAMH 10579 *isolata ex ligno brunneo-putrefacto piceae marianae in sphagno palustro submersae.*

Colonies on OA 40-45 mm diam at 28 days at 15 °C, white, floccose, pale orange exudate produced; aerial hyphae and conidia abundant, white to off-white or pale gray; reverse orange. Colonies on CMA 44-48 mm diam at 28 days and 15 °C, appressed, colourless, consisting mostly of immersed, hyaline hyphae; reverse colourless. Aerial conidia sparse, concentrated in the center of the colony, initially white, becoming pink with age. Ascomata produced after 6-8 months on CMA at 15°C. Ascomata solitary or clumped, globose to subglobose, red to red-brown at maturity, 150-400 µm diam. Peridial hyphae red brown (Figure 5.3A), septate, thick walled, 2-2.5 µm diam, coarsely asperulate, highly branched and anastomosing to form a dense reticuloperidium (Figures 5.3A, 5.4A). Distinct appendages absent but peridial hyphae terminate in swollen, thin-walled, subhyaline, verruculose apices, 5-10 x 3-4 µm (Figure 5.3A). Asci 8-spored, hyaline, globose to subglobose, solitary or borne in chains (Figure 5.4B), deliquescent, 5-8 µm diam (Figures 5.3B, 5.4B,C). Ascospores broadly fusoid to ellipsoidal, hyaline, thick-walled, irregularly asperulate to verruculose at maturity, 3-5 x 2-3 µm (Figure 5.4C). Anamorph: *Geomyces* sp. (Figure 5.3C,D, 5.4D,E). Conidiophores erect, hyaline, thin- and smooth-walled, dendritic with verticillate branching, 5-25 x 1-1.5 µm, branches fragmenting basipetally to form rhexolytically dehiscent arthroconidia (Figure 5.3C). Conidia white to pale pink *en masse*. Aleurioconidia terminal, subglobose to broadly pyriform with prominent truncate basal scars, relatively thick-walled, hyaline to lightly pigmented, asperulate (Figure 5.4D) or irregularly verrucose (Figures 5.3D, 5.4D,E) at maturity, 2.5-4 x 2-3 µm. Intercalary conidia subglobose to elongate and barrel-shaped with more or less truncate ends, thick-walled, hyaline to lightly pigmented, asperulate or irregularly verrucose at maturity, 2.5-5 x 2-3 µm.

Holotype: Dried culture of isolate UAMH 10579 from brown-rotted black spruce wood buried under *Sphagnum* peat. Holotype and *ex*-type are deposited as UAMH 10579.

Other material: **Canada**. Alberta: 5 km east of Perryvale (54° 28' N, 113° 16' W), *Picea mariana-Sphagnum fuscum* bog, ex brown-rotted spruce wood bait, July 2002, A. Rice (UAMH 10580).

Key to species of *Pseudogymnoascus*

1. Colonies white with yellow reverse. Yellow exudate present. Ascomata with smooth-walled, orange peridial hyphae and long (40-120 µm), smooth- and thick-walled, branched appendages. Ascospores smooth or with a faint longitudinal rim..............*P. appendiculatus*

1. Colonies white to pink or vinaceous; reverse not yellow. Yellow exudates absent. Ascomata with rough, red to red-brown peridial hyphae and short (<50 µm), subhyaline, thin- and rough-walled, unbranched appendages. Ascospores either smooth or irregularly ornamented, lacking a longitudinal rim..2

2. Ascospores smooth walled..*P. roseus* var. *roseus*

2. Ascospores ornamented..3

3. Colonies vinaceous or grayish-red. Ascomata abundant. Appendages 20-54 µm long. Ascospores lobate-reticulate, 2.5-4 x 2-25. µm. Conidia smooth-walled only...*P. roseus* var. *ornatus*

3. Colonies white to pink. Ascomata scarce. Appendages 5-10 µm long. Ascospores verrucose, 3-5 x 2-3 µm. Conidia smooth to asperulate or covered with large warts.........*P. verrucosus*

5.3.2. DNA Sequencing

Sequences of ITS 1, 5.8S subunit, and ITS 2 ranged from 503 to 545 bases. Manual alignment yielded a total length of 528 characters. Of these, 378 were constant, 85 were variable but parsimony-uninformative, and 65 were parsimony-informative. Three most parsimonious trees were obtained using the heuristic random sequence addition search option with gaps treated as missing characters. One of these, with a length of 218, a consistency index of 0.835, a retention index of 0.914, and a homoplasy index of 0.165, is shown in Figure 5.5.

Species of *Pseudogymnoascus, Gymnostellatospora*, and *Geomyces* formed a well-supported clade (bootstrap 86) after one isolate identified as *Geomyces* sp. (UAMH 7253) was excluded. This clade included two groups with strong support (Figure 5.5). The first group (bootstrap 98) included all sequenced species of *Gymnostellatospora* and *Geomyces asperulatus*, with a well-supported subclade (bootstrap 89) including all of the *Gymnostellatospora* isolates except UAMH 9339 (*Gy. alpina*), which formed a clade (bootstrap 68) with *G. asperulatus*. The second group (bootstrap 94) included all sequenced *Pseudogymnoascus* species, *Geomyces* *pannorum* isolates, and one isolate identified as *Geomyces* sp. (UAMH 9107). The three isolates of *P. appendiculatus* formed an extremely well-supported clade (bootstrap 100) within this group as did the four isolates of *P. roseus* (bootstrap 98). The two isolates of *P. verrucosus* formed a clade with relatively low bootstrap support (58) despite differing at less than 1% of the bases. *Geomyces* was polyphyletic: *G. asperulatus* was monophyletic (bootstrap 98) and allied with *Gymnostellatospora*, *G. pannorum* was paraphyletic and grouped with *Pseudogymnoascus*, and at least one species was not allied with either teleomorph genus.

5.4. Discussion

Species of *Pseudogymnoascus* have small (less than 5 μm long), ellipsoidal to fusiform ascospores and *Geomyces* anamorphs. *Pseudogymnoascus appendiculatus* is morphologically distinct because it has smooth, orange peridial hyphae and long, concolorous, smooth, branched appendages, while other species have asperulate to verrucose, red peridial hyphae and short, hyaline, unbranched appendages. Ascomata of *P. appendiculatus* are larger than those of the two varieties of *P. roseus* and its ascospores are smooth except for a longitudinal rim, which is narrow and indistinct, compared to the wide, wing-like crests on species of *Gymnostellatospora* (Sigler *et al.* 2000). *Pseudogymnoascus verrucosus* is morphologically similar to the two varieties of *P. roseus* in having red, asperulate peridial hyphae that terminate in short, subhyaline appendages and ascospores that lack a longitudinal rim (Tsuneda 1982, Udagawa & Uchiyama 1999, Sigler *et al.* 2000). However, the ascospores of *P. roseus* var. *roseus* are smooth-walled (Tsuneda 1982, Sigler *et al.* 2000) and those of *P. roseus* var. *ornatus* have a network of irregular ridges producing lobate-reticulate ornamentation (Udagawa & Uchiyama 1999) while those of *P. verrucosus* have an irregularly warty membrane that gives them a verrucose appearance. The peridial hyphae of *P. verrucosus* are more ornamented than those of *P. roseus*, appearing warty rather than minutely asperulate under light microscopy. The appendages of *P. roseus* var. *ornatus* are more than twice as long as those of *P. verrucosus* (Udagawa & Uchiyama 1999) while those of *P. roseus* var. *roseus* are clavate rather than slightly swollen and are produced at the apices of dichotomous branches (Sigler *et al.* 2000). The most distinctive feature of *P. verrucosus* is the presence of two types of barrel-shaped to pyriform conidia: some are minutely asperulate and resemble the anamorphs of other *Pseudogymnoascus* species while others are covered with large, irregular warts.

Asci are produced in short chains and develop at different rates in both of the new species. Asynchronous development of asci was noted in *P. roseus* by Tsuneda (1982) but the development of asci in chains has not been noted previously in either *Pseudogymnoascus* or

Gymnostellatospora (Tsuneda 1982, Udagawa *et al.* 1993, Uchiyama *et al.* 1995, Udagawa 1997, Udagawa & Uchiyama 1999, 2000, Sigler *et al.* 2000). The pattern of development observed in the two new species contrasts sharply with that observed in *Myxotrichum deflexum* Berkeley (Rosing 1985) and *M. arcticum* Udagawa, Uchiyama & Kamiya (Tsuneda & Currah 2004) where asci arise individually from penultimate cells of croziers and develop more or less synchronously. Tsuneda and Currah (2004) suggest that ascus development in *M. arcticum* is more typical of leotiomycete fungi rather than eurotiomycete fungi and supports placement of the family within the inoperculate discomycetes. However, the phylogenetic importance of this character is called into question by the presence of chains of asci in *Pseudogymnoascus*, which is also affiliated with the *Leotiomycetes*. Despite the apparent phylogenetic distance between the two lineages traditionally included in the *Myxotrichaceae*, they are morphologically and ecologically similar, suggesting convergent evolution, possibly for dispersal by insect vectors in similar habitats (Currah 1985, 1994, Greif & Currah 2003). Additional phylogenetic studies using multiple genes are needed to determine the precise relationship between these lineages and their placement within the *Leotiomycetes*.

Two characters, ascospore ornamentation and anamorphs, have been used traditionally to delimit *Pseudogymnoascus* and *Gymnostellatospora*. Raillo (1929) erected *Pseudogymnoascus* (*Gymnoascaceae*) for two species (*P. roseus* and *P. vinaceus* Raillo) from soil in the Soviet Union. Two additional species were described from soil in the Soviet Union and Canada before 1980: *P. caucasicus* Cejp & Milko (Cejp & Milko 1966) and *P. bhatti* Samson (Samson 1972). All four of these species have smooth ascospores and *Geomyces* anamorphs and these two characters were considered diagnostic for the genus (Samson 1972, Orr 1979, Currah 1985). Currah (1985) considered the four species synonyms and gave priority to *P. roseus*. In 1982, two species were described with ridged ascospores and poorly developed anamorphs: *P. dendroideus* Locquin-Linard from cow dung in Algeria (Locquin-Linard 1982) and *P. alpinus* Müller & von Arx from the rhizosphere of *Erica carnea* L. (Müller & von Arx 1982). Currah (1985) did not mention these species, but von Arx (1987) included them in the genus and noted the correlation between ascospore ornamentation and anamorph presence. Udagawa *et al.* (1993) considered these differences significant at the generic level and erected *Gymnostellatospora* to accommodate species with ornamented ascospores and no anamorphs. Between 1993 and 2000, five species were described from Japanese and Russian soils and rotting wood in Canada: *Gy. japonica* (Udagawa *et al.* 1993), *Gy. frigida* (Uchiyama *et al.* 1995), *Gy. canadensis*, *Gy. subnuda* (Sigler *et al.* 2000), and *Gy. parvula* (Udagawa & Uchiyama 2000). Udagawa (1997) also transferred *P. dendroideus* and *P. alpinus* into *Gymnostellatospora* as *Gy. dendroidea* and *Gy. alpina* respectively. The distinctions between the genera were blurred by the description of *P. roseus* var. *ornatus* with ornamented ascospores and a *Geomyces* anamorph (Udagawa & Uchiyama 1999). Sigler *et al.* (2000) upheld the generic delimitations, despite the presence of ornamented ascospores in *P. roseus* var. *ornatus* and anamorphs in *Gy. alpina, Gy. frigida,* and *Gy. canadensis*, noting that none of these anamorphs was a *Geomyces* state characteristic of *Pseudogymnoascus* and that the ascospores of *P. roseus* var. *ornatus* lacked the longitudinal ridges and crests characteristic of *Gymnostellatospora*. However, they suggested that the species of *Pseudogymnoascus* and *Gymnostellatospora* might occur along a gradient and that further research involving DNA sequence analyses were required to determine the distinction of the genera (Sigler *et al.* 2000).

The distinctions between the two genera are blurred further by the description of *P. appendiculatus* with a *Geomyces* anamorph and a faint longitudinal band on its ascospores. The presence of this, and other "intermediate" taxa (*P. roseus* var. *ornatus* and *P. verrucosus*), prompted my phylogenetic assessment of the two genera. DNA sequence analyses of the ITS 1, 5.8S, and ITS 2 regions of the rDNA support the generic distinction of *Gymnostellatospora* and *Pseudogymnoascus* with most isolates of *Geomyces* included in the *Pseudogymnoascus* clade. Notably, one undescribed species of *Geomyces* was not included in either clade and another species, *G. asperulatus*, was included in the *Gymnostellatospora* clade, suggesting that the presence of a *Geomyces* anamorph is not restricted to species of *Pseudogymnoascus*. Meanwhile, ascospores with a pronounced longitudinal band and ridges are characters exclusive to *Gymnostellatospora*. The two genera are retained and the definitive character is the presence of longitudinal bands and striations (ridges) on the ascospores of *Gymnostellatospora* species.

Species-level relationships are reasonably well-supported in *Pseudogymnoascus*. *Pseudogymnoascus appendiculatus*, *P. roseus*, and *P. verrucosus* appea distinct and *P. roseus* and *P. verrucosus* appear more closely related to each other than to *P. appendiculatus*. Bootstrap support for *P. verrucosus* was much lower than for *P. appendiculatus* and *P. roseus* although the percentage difference in bases was similar and lower than 1% within all three species. Consistent morphological characters, including the unique warted conidia, further support conspecificity. Cultures of *P. roseus* var. *ornatus* are not available for sequencing so its relationship to the type variety cannot be determined. Relationships among isolates of *Geomyces* are not well resolved but the genus is clearly polyphyletic and further molecular, morphological, and physiological studies on a greater number of isolates are required to elucidate relationships and distinguishing characters among these taxa and to determine their placement within the *Ascomycota*.

Relationships among species of *Gymnostellatospora* were not well resolved and more isolates of each species need to be sampled.

Myxotrichaceous fungi, including *Geomyces* and *Oidiodendron* species, were among the most frequently isolated fungi from Perryvale Bog (Rice & Currah 2002, unpublished) and their abundance suggests that they may be important saprobes in this ecosystem. Most records of taxa in this family are from soil, peat, and decaying wood and other organic matter in cool, temperate environments (e.g. Barron 1962, Barron & Booth 1966, Cejp & Milko 1966, Samson 1972, Udagawa *et al.* 1993, Hambleton *et al.* 1998, Sigler & Flis 1998, Udagawa & Uchiyama 1999, Sigler *et al.* 2000, Rice & Currah 2002, in press). *In vitro* physiological studies support the assertion that they are important saprobes in soil, decaying wood, and peat in temperate and cool environments. Most of these fungi are cellulolytic and many are psychrophilic or psychrotolerant (e.g. Currah 1985, Udagawa *et al.* 1993, Uchiyama *et al.* 1995, Udagawa & Uchiyama 1999, Sigler & Currah 2000, Rice & Currah, in press). Some species also degrade other plant, animal, and fungal residues, including polyphenolic polymers, pectin, starch, chitin, gelatin, and lipids that are common in peat, wood, and organic soils (Rice & Currah 2001, in press). In addition to the saprobic lifestyle, some *Myxotrichaceae*, including *P. roseus* (Dalpé 1989), have been shown to form ericoid mycorrhizal associations *in vitro* (e.g. Dalpé 1986, 1989, 1991) and it is possible that at least some of them may also occupy a mycorrhizal role in peatlands.

Table 5.1. Species, strain, and collection information for species of *Pseudogymnoascus*, *Gymnostellatospora*, and *Geomyces* where the internal transcribed spacer (ITS) and 5.8S regions of the nuclear ribosomal DNA are newly sequenced.

Species	Strain	GenBank	Collection Information
G. asperulatus	UAMH 183[t]	DQ117444	Forest soil, USA, Raymond
G. asperulatus	UAMH 9032	DQ117449	Decayed spruce, Canada, Lumley
G. pannorum	UAMH 714	DQ117446	Human, Netherlands, De Vries
G. pannorum	UAMH 1030	DQ117436	Cold storage food, USA, Kuehn
G. pannorum	UAMH 1088	DQ117442	Frozen food, USA, Kuehn
Geomyces sp.	UAMH 7253	DQ117447	Human sputum, Canada, Rennie
Geomyces sp.	UAMH 9107	DQ117450	Decayed spruce, Canada, Lumley
Gy. alpina	UAMH 9339	DQ117458	Alpine forest soil, Kenya, Udagawa
Gy. alpina	UAMH 9430[t]	DQ117459	*Erica carnea* rhizosphere, Switzerland, Müller
Gy. canadensis	UAMH 8899[t]	DQ117448	Decayed spruce, Canada, Lumley
Gy. canadensis	UAMH 9238[p]	DQ117453	Decayed spruce, Canada, Lumley
Gy. frigida	UAMH 9304[t]	DQ117457	Alpine forest soil, Japan, Udagawa
Gy. japonica	UAMH 9239	DQ117454	Decayed spruce, Canada, Lumley
Gy. japonica	UAMH 9240	DQ117455	Decayed spruce, Canada, Lumley
Gy. subnuda	UAMH 9242[p]	DQ117456	Decayed spruce, Canada, Lumley
P. appendiculatus	UAMH 10510	DQ117437	*Sphagnum* bog, Canada, Rice
P. appendiculatus	UAMH 10511	DQ117438	*Sphagnum* bog, Canada, Rice
P. appendiculatus	UAMH 10512	DQ117439	*Sphagnum* bog, Canada, Rice
P. roseus	UAMH 1658	DQ117443	Forest soil, Ghillini
P. roseus	UAMH 2879	DQ117445	Alpine soil, Canada, Widden
P. roseus	UAMH 9163	DQ117451	Ectomycorrhizal root, Canada, Fernando
P. roseus	UAMH 9222	DQ117452	Decayed spruce, Canada, Lumley
P. verrucosus	UAMH 10579[t]	DQ117440	*Sphagnum* bog, Canada, Rice
P. verrucosus	UAMH 10580[p]	DQ117441	*Sphagnum* bog, Canada, Rice

[t] *ex*-type culture

[p] *ex*-para-type culture

Figure 5.1. Light micrographs of *Pseudogymnoascus appendiculatus* direct mounts from cultures grown on cornmeal agar (CMA) at 5°C in the dark.

A. Ascocarp with smooth, peridial hyphae and long, branched appendages. Bar = 80 µm. **B**. Smooth, thick-walled, peridial hyphae with long, branched appendages. Bar = 40 µm. **C**. Smooth peridial hyphae with ascospores and asci containing developing ascospores (arrow). Bar = 15 µm. **D**. Ellipsoidal ascospores with longitudinal band or rim (arrows). Bar = 15 µm. **E**. *Geomyces* anamorph with verticillately branched solitary conidiophores bearing small, barrel-shaped or pyriform aleurioconidia and arthroconidia. Bar = 15 µm. **F**. Long chains of barrel-shaped to pyriform arthroconidia. Bar = 15 µm. **G**. Synnematous bundle of conidiophores bearing pyriform aleurioconidia. Bar = 15 µm.

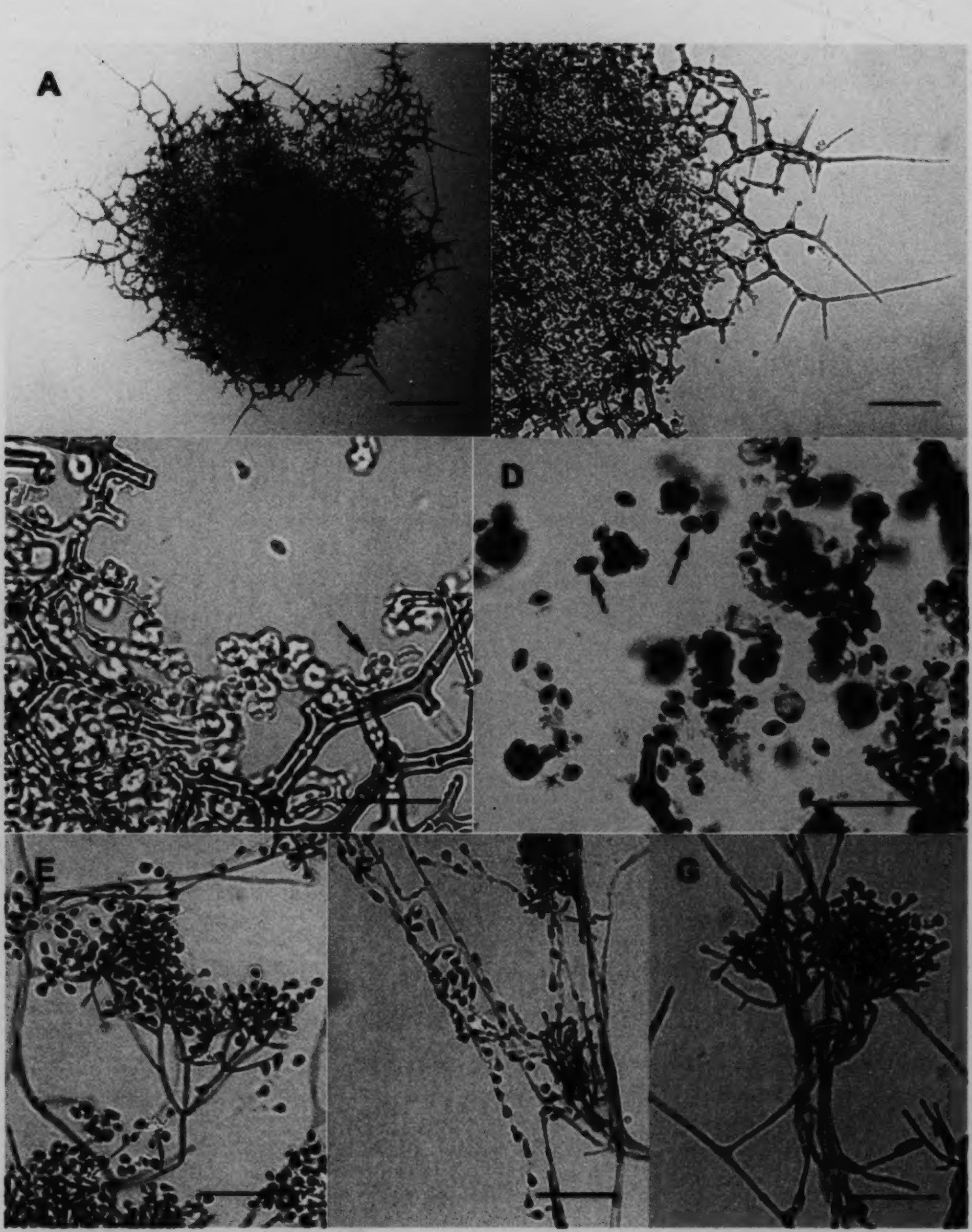

A
C
D
E
G

Figure 5.2. Scanning electron micrographs of *Pseudogymnoascus appendiculatus* obtained from cultures grown on cornmeal agar (CMA) at 5°C in the dark.

A. Ascocarp with long, smooth, branched, appendages. Bar = 100 µm. **B**. Peridial hyphae and long, smooth, branched appendages. Bar = 10 µm. **C**. Young ascus. Note clavate shape. Bar = 2 µm. **D**. Chain of immature asci at different stages of development. Note the variation in ascus shape. Bar = 2.5 µm. **E**. Subglobose to globose, developing ascus containing ascospores close to maturity. Bar = 1 µm. **F**. Ascus rupturing to release ascospores. Note the faint longitudinal rim on the ascospores (arrow). Bar = 2.5 µm. **G**. Mature ascospores with remnants of ascus. Arrow indicates faint longitudinal band on the ascospore. Bar = 1 µm. **H**. *Geomyces* anamorph with pyriform, minutely asperulate aleurioconidia. Bar = 1 µm. **I**. Synnematous bundle of conidiophores bearing pyriform, minutely asperulate conidia. Bar = 5 µm.

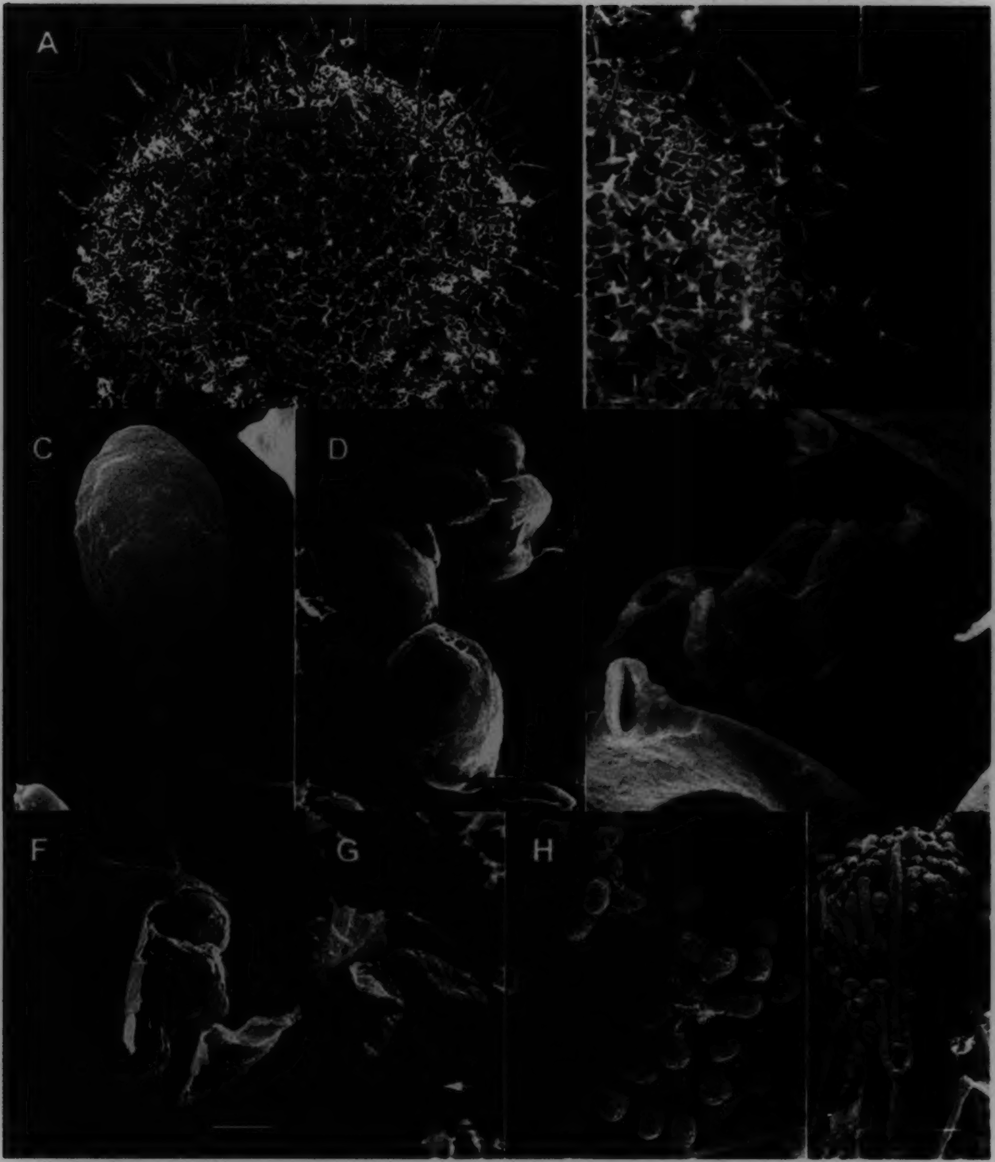

A
C
D
F
G
H

Figure 5.3. Light micrographs of *Pseudogymnoascus verrucosus* direct mounts from cultures grown on cornmeal agar (CMA) at 15°C in the dark.

A. Verrucose peridial hyphae terminating in short, subhyaline apices (arrow). Bar = 40 µm. **B**. Ascus containing ascospores (arrow). Bar = 15 µm. **C**. *Geomyces* anamorph with short, verticillately branched conidiophores bearing pyriform aleurioconidia. Bar = 15 µm. **D**. Thick-walled, rough conidia. Bar = 15 µm.

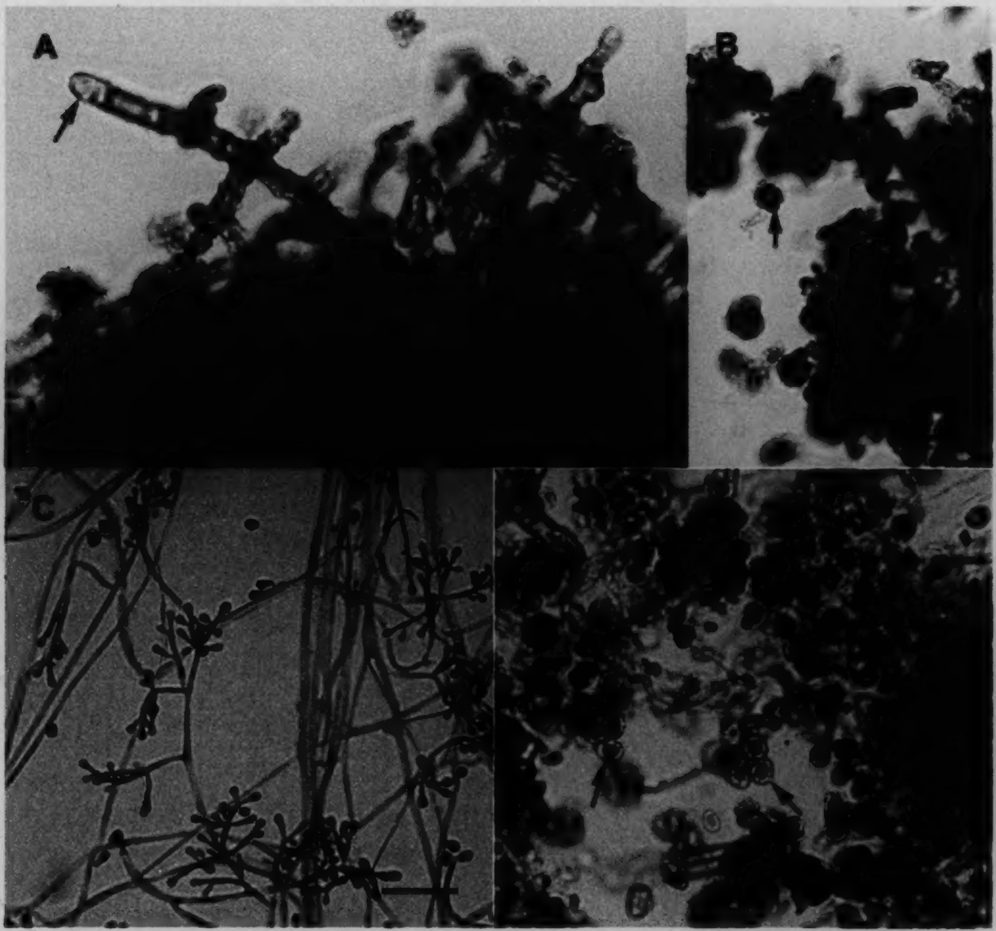

A
B
C

Figure 5.4. Scanning electron micrographs of *Pseudogymnoascus verrucosus* obtained from cultures grown on cornmeal agar (CMA) at 15°C in the dark.

A. Highly branched and anastomosed, coarsely asperulate to verrucose peridial hyphae. Bar = 10 µm. **B**. Chains (C) of subglobose to globose asci at different stages of development. Note the ruptured ascus (arrowhead) and scars left by the dehiscence of adjacent asci (arrow). Bar = 10 µm. **C**. Asperulate to warty ascospores surrounded by remnants of the ascus. Bar = 1 µm. **D**. Two types of conidia: *Geomyces* anamorph with pyriform, minutely asperulate aleurioconidia (C), and pyriform to irregular conidia covered with large, irregular warts (arrow and arrowhead). Note that many of the warts are in the process of collapsing (arrowhead). Bar = 1 µm. **E**. Two irregularly shaped, warty conidia in a short chain. Note that the warts have collapsed. Bar = 1 µm.

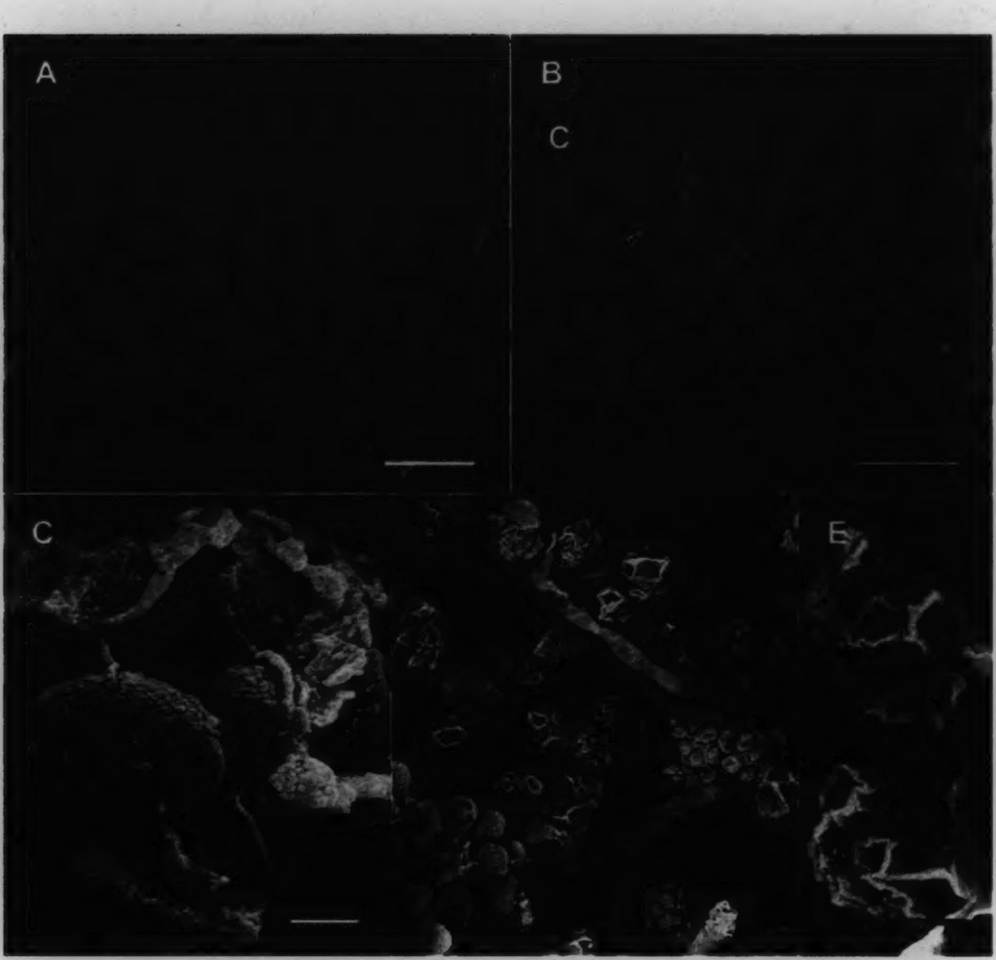
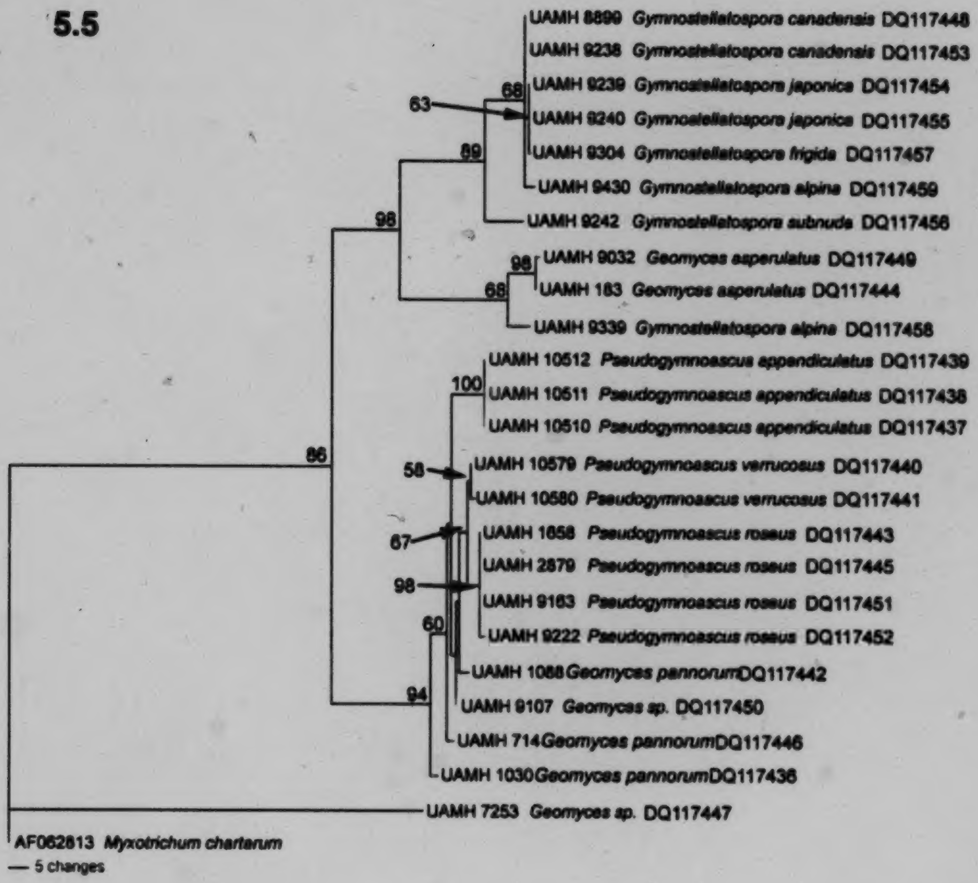

A
B
C
C
E

Figure 5.5. One of three most parsimonious trees from sequence analysis of the ITS 1, 5.8S, and ITS 2 regions of the nuclear ribosomal DNA of *Pseudogymnoascus, Geomyces,* and *Gymnostellatospora* species and *Myxotrichum chartarum*. Bootstrap values less than 50 are not shown.

5.5


UAMH 8899 *Gymnostellatospora canadensis* DQ117448
UAMH 9238 *Gymnostellatospora canadensis* DQ117453
UAMH 9239 *Gymnostellatospora japonica* DQ117454
UAMH 9240 *Gymnostellatospora japonica* DQ117455
UAMH 9304 *Gymnostellatospora frigida* DQ117457
UAMH 9430 *Gymnostellatospora alpina* DQ117459
UAMH 9242 *Gymnostellatospora subnuda* DQ117456
UAMH 9032 *Geomyces asperulatus* DQ117449
UAMH 183 *Geomyces asperulatus* DQ117444
UAMH 9339 *Gymnostellatospora alpina* DQ117458
UAMH 10512 *Pseudogymnoascus appendiculatus* DQ117439
UAMH 10511 *Pseudogymnoascus appendiculatus* DQ117438
UAMH 10510 *Pseudogymnoascus appendiculatus* DQ117437
UAMH 10579 *Pseudogymnoascus verrucosus* DQ117440
UAMH 10580 *Pseudogymnoascus verrucosus* DQ117441
UAMH 1658 *Pseudogymnoascus roseus* DQ117443
UAMH 2879 *Pseudogymnoascus roseus* DQ117445
UAMH 9163 *Pseudogymnoascus roseus* DQ117451
UAMH 9222 *Pseudogymnoascus roseus* DQ117452
UAMH 1088 *Geomyces pannorum* DQ117442
UAMH 9107 *Geomyces sp.* DQ117450
UAMH 714 *Geomyces pannorum* DQ117446
UAMH 1030 *Geomyces pannorum* DQ117436
UAMH 7253 *Geomyces sp.* DQ117447
AF062813 *Myxotrichum chartarum*
5 changes
68
63
89
98
98
68
100
86
58
67
98
60
94

5.5. Literature Cited

Barron GL (1962). New species and new records of *Oidiodendron*. *Canadian Journal of Botany* **40**: 589–607.

Barron GL, Booth C (1966). A new species of *Arachniotus* with an *Oidiodendron* conidial state. *Canadian Journal of Botany* **44**: 1057–1061.

Carmichael JW (1962). *Chrysosporium* and some other aleurosporic hyphomycetes. *Canadian Journal of Botany* **40**: 1137–1173.

Cejp K, Milko AA (1966). Genus *Pseudogymnoascus* Raillo (*Gymnoascaceae*). Českà Mykologie **20**: 160–163.

Cubero OF, Crespo A, Fatehi J, Bridge PD (1999). DNA extraction and PCR amplification method suitable for fresh, herbarium-stored, lichenized, and other fungi. *Plant Systematics and Evolution* **216**: 243–249.

Currah RS (1985). Taxonomy of the *Onygenales*: *Arthrodermataceae, Gymnoascaceae, Myxotrichaceae* and *Onygenaceae*. *Mycotaxon* **24**: 1–216.

Currah RS (1994). Peridial morphology and evolution in the prototunicate ascomycetes. In: Hawksworth DL (ed) *Ascomycete Systematics: Problems and Perspectives in the Nineties*. Plenum Press, New York. pp 281–293.

Dalpé Y (1986). Axenic synthesis of ericoid mycorrhiza in *Vaccinium angustifolium* Ait. by *Oidiodendron* species. *New Phytologist* **103**: 391–396.

Dalpé Y (1989). Ericoid mycorrhizal fungi in the *Myxotrichaceae* and *Gymnoascaceae*. *New Phytologist* **113**: 523–527.

Dalpé Y (1991). Statut endomycorrhizien du genre *Oidiodendron*. *Canadian Journal of Botany* **69**: 1712–1714.

Felsenstein J (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**: 783–791.

Gibas CFC, Sigler L, Summerbell RC, Currah RS (2002). Phylogeny of the genus *Arachnomyces* and its anamorphs and the establishment of *Arachnomycetales*, a new eurotiomycete order in the *Ascomycota*. *Studies in Mycology* **47**: 131–139.

Greif MD, Currah RS (2003). A functional interpretation of the role of the reticuloperidium in whole-ascoma dispersal by arthropods. *Mycological Research* **107**: 77–81.

Hambleton S, Egger KN, Currah RS (1998). The genus *Oidiodendron*: species delimitation and phylogenetic relationships based on nuclear ribosomal DNA analysis. *Mycologia* **90**: 854–869.

Locquin-Linard M (1982). *Pseudogymnoascus dendroideus* Locquin-Linard, nouvelle espèce de Gymnoascale (Ascomycètes) coprophile d'Afrique du Nord. *Cryptogamie, Mycologie* **3**: 409–414.

Lumley TC, Gignac LD, Currah RS (2001). Microfungus communities of white spruce and trembling aspen logs at different stages of decay in disturbed and undisturbed sites in the boreal mixedwood region of Alberta. *Canadian Journal of Botany* **79**: 76–92.

Mori Y, Sato Y, Takamatsu S (2000). Molecular phylogeny and radiation time of *Erysiphales* inferred from the nuclear ribosomal DNA sequences. *Mycoscience* **41**: 437–447.

Müller E, von Arx JA (1982). *Pseudogymnoascus alpinus* nov. spec. *Sydowia* **35**: 135–137.

Mori Y, Sato Y, Takamatsu S (2000). Molecular phylogeny and radiation time of *Erysiphales* inferred from the nuclear ribosomal DNA sequences. *Mycoscience* **41**: 437–447.

Orr GF (1979). The genus *Pseudogymnoascus*. *Mycotaxon* **8**: 165–173.

Raillo A (1929). Beiträge zur Kenntnis der Boden-Pilze. *Zentralblatt fur Bakteriologie und Parasitenkunde Jena Abt. 2.* **78**: 515–524.

Rice AV, Currah RS (2001). Physiological and morphological variation in *Oidiodendron maius*. *Mycotaxon* **79**: 383–396.

Rice AV, Currah RS (2002). New perspectives on the niche and holomorph of the myxotrichoid hyphomycete, *Oidiodendron maius*. *Mycological Research* **106**: 1463–1467.

Rice AV, Currah RS (in press 1). *Oidiodendron*: A survey of the named species and related anamorphs of *Myxotrichum*. *Studies in Mycology* (accepted Feb. 2005).

Rosing WC (1985). Fine structure of cleistothecia, asci, and ascospores of *Myxotrichum deflexum*. *Mycologia* **77**: 920-926.

Samson RA (1972). Notes on *Pseudogymnoascus, Gymnoascus*, and related genera. *Acta Botanica Neerlandica* **21**: 517–527.

Sigler L, Flis A (1998). *Catalogue of the University of Alberta Microfungus Collections and Herbarium*, 3rd Edition. University of Alberta, Edmonton, AB, Canada. (available online at www.devonian.ualberta.ca/uamh)

Sigler L, Lumley TC, Currah RS (2000). New species and new records of saprophytic ascomycetes (*Myxotrichaceae*) from decaying logs in the boreal forest. *Mycoscience* **41**: 495–502.

Sugiyama S, Ohara A, Mikawa T (1999). Molecular phylogeny of onygenalean fungi based on small subunit ribosomal DNA (SSU rDNA) sequences. *Mycoscience* **40**: 251–258.

Swofford DL (2002). PAUP*: phylogenetic analysis using parsimony (*and other methods), Version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.

Tsuneda A (1982). Scanning electron microscopy of *Pseudogymnoascus roseus*. *Mycologia* **74**: 844–847.

Tsuneda A, Currah RS (2004). Ascomatal morphogenesis in *Myxotrichum arcticum* supports the derivation of the *Myxotrichaceae* from a discomycetous ancestor. *Mycologia* **96**: 627–635.

Tsuneda A, Thormann MN, Currah RS (2001). Modes of cell wall degradation of *Sphagnum fuscum* by *Acremonium* cf. *curvulum* and *Oidiodendron maius*. *Canadian Journal of Botany* **79**: 93–100.

Uchiyama S, Kamiya S, Udagawa S (1995). Five onygenalean fungi from Japan. *Mycoscience* **36**: 211–220.

Udagawa S (1997). Taxonomic studies on Plectomycetes (cleistothecial ascomycetes). *Transactions of the Mycological Society of Japan* **38**: 143–157.

Udagawa S, Uchiyama S (1999). Taxonomic studies on new or critical fungi of non-pathogenic *Onygenales* 1. *Mycoscience* **40**: 277 – 290.

Udagawa S, Uchiyama S (2000). Two onygenalean fungi from Russian Far East soil. *Mycoscience* **41**: 217–221.

Udagawa S, Uchiyama S, Kamiya S (1993). *Gymnostellatospora*, a new genus of the *Myxotrichaceae*. *Mycotaxon* **48**: 157–164.

von Arx JA (1987). A re-evaluation of the *Eurotiales*. *Persoonia* **13**: 273–300.

White TJ, Bruns TD, Lee SB, Taylor JW (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds.) *PCR Protocols: A guide to the methods and applications*. Academic Press, New York, USA. pp. 315–322.

CHAPTER 6: *IN VITRO* DECOMPOSITION OF *SPHAGNUM* BY MICROFUNGI RESEMBLES WHITE ROT OF WOOD[5]

6.1. Introduction

Peatlands cover about 4% of the world's ice-free land area (e.g. Gorham 1991, Vitt 1994) but store one quarter to one third of global soil carbon (Gorham 1991, Limpens & Berendse 2003) due to extremely slow decomposition of their constituent vegetation (e.g. Clymo 1965, Vitt 1994, Verhoeven & Liefveld 1997, Limpens & Berendse 2003). Among peatland plants, *Sphagnum* L. mosses are particularly resistant to decay and, consequently, *Sphagnum*-dominated peatlands store more carbon than any other peatland type (Verhoeven & Liefveld 1997).

Environmental conditions in peatlands, including low temperatures, acidity, and anoxia, contribute to the slow decomposition of *Sphagnum* remains (Clymo 1965, Gorham 1991, Vitt 1994). However, *Sphagnum* decomposes slowly even in more favorable environments (Verhoeven & Liefveld 1997, Limpens & Berendse 2003) because intrinsic factors, such as high water-holding and cation-exchange capacities, and inhibitory organochemicals, including phenolics, organic acids, and lipids, inhibit the activities of decay organisms (Limpens & Berendse 2003). As a result, the aerated surface peat in *Sphagnum*-dominated peatlands consists primarily of the remains of *Sphagnum* mosses with smaller amounts of woody and herbaceous plant debris (Verhoeven & Liefveld 1997, Domisch *et al.* 2000, Williams & Yavitt 2003). *Sphagnum* leaves are one-cell thick and consist of a network of small, chlorophylous "green cells" that surround larger, trapezoidal, achlorophylous, dead "hyaline cells" that have large, circular pores and bands of cell-wall thickenings (Schofield 2001). Hyaline cells resemble the xylary elements in wood because cell walls consist of cellulose microfibrils embedded in an amorphous network of phenolic polymers (Verhoeven & Liefveld 1997). In the walls of xylem cells, the amorphous network is rigid and is primarily composed of lignin while in *Sphagnum*, it is flexible and composed of a variety of phenolic compounds, tannins, and pectin-like "sphagnan" (Verhoeven & Liefveld 1997). A lipid coating on the hyaline cells further protects them from decay (Verhoeven & Liefveld 1997).

Three main types of wood decay, i.e., white rot, brown rot, and soft rot, have been described (Blanchette 1995). White rot, caused primarily by basidiomycetes (Blanchette 1995, Reid 1995), but also ascomycetes in the *Xylariaceae* (Osono & Takeda 2002), is characterized by the removal of all cell-wall components, including lignin (Blanchette 1995, Reid 1995, Osono & Takeda 2002). Some white-rot fungi degrade all the components simultaneously while others preferentially attack lignin (Blanchette 1995, Reid 1995). In brown rot, also caused primarily by basidiomycetes, cellulose and other polysaccharides are selectively removed from wood and there is limited degradation of lignin (Blanchette 1995). Ascomycetes that cause soft rot remove cellulose, polysaccharides, and in some cases lignin from the outer layers of the cell walls while leaving the middle lamellae intact (Blanchette 1995). Structural similarities between the walls of *Sphagnum* hyaline cells and woody plants led to the hypothesis that similar decay patterns, particularly soft- and white-rot, should be observed in *Sphagnum*.

---

[5] A version of this chapter has been submitted for publication: Rice AV, Tsuneda A, Currah RS (submitted) *In vitro* decomposition of *Sphagnum* by some microfungi resembles white rot of wood. *FEMS Microbiology Ecology* (submitted July 2005).

Approximately 650 species of microfungi, including chytrids, zygomycetes, ascomycetes, and basidiomycetes, have been isolated from peatlands in Europe and the Americas (see Thormann, in press 1, 2). Over 400 are asexual fungi with affinities to the ascomycetes while less than five percent are basidiomycetes (Thormann, in press 1). There have been extensive microfungal collections from *Sphagnum* peat from "Perryvale Bog", a black spruce-*Sphagnum fuscum* (Schimp.) Klinggr. bog 5 km east of Perryvale, Alberta, Canada (e.g. Thormann *et al.* 1999, 2001b, 2004b, Tsuneda *et al.* 2000, Rice & Currah 2002, in prep, Thormann, in press 1,2). Members of the ascomycete family *Myxotrichaceae* were among the most frequently observed fungi on lignocellulose-rich bait blocks placed in Perryvale Bog for 8-12 months (Table 6.1). Most of these fungi are cellulolytic and have been reported previously from decaying wood and wood pulp (e.g. Robak 1932, Melin & Nannfeldt 1934, Sigler & Flis 1998, Sigler *et al.* 2000, Lumley *et al.* 2001). While reports of basidiomycetes are much less common from peatlands (see Thormann, in press 1), white-rot fungi, including *Bjerkandera adusta* (Wildenow) Karsten, have been isolated from Perryvale Bog (Thormann *et al.* 2001b, 2004b). The abilities of representative *Myxotrichaceae* from Perryvale Bog to degrade cellulose, tannic acid, lignin, and *Sphagnum*-specific phenolics, and to cause mass losses of *Sphagnum* were examined. Scanning electron microscope (SEM) examination of patterns of leaf cell wall decay permitted direct comparison with two white-rot fungi, *Bjerkandera adusta* and *Phanerochaete chrysosporium* Burdsall, a well studied wood-decay fungus with a reproductive morphology similar to the *Myxotrichaceae*.

6.2. Methods

6.2.1. Isolation of Fungi

During a survey of lignin- and cellulose-degrading fungi from peat, lignin-rich, brown-rotted spruce bait blocks were placed 5-10 cm beneath the peat surface in Perryvale Bog for 8-12 months. Small fragments of the blocks were flamed then placed in moist chambers or plated onto cornmeal agar [17 g BBL cornmeal agar (Becton Dickinson Co., Sparks, MD), 1 l dH_2O] amended with 0.4% benomyl [Methyl 1-(butycarbamoyl)-2-benzimidazolecarbamate (Sigma Chemical Co., St. Louis, MO)] (CMAB), or Mycosel® agar [MYCO; 36 g BBL Mycosel agar (Becton Dickinson Co.), 1 l dH_2O]. Plates were observed for one year and fungi were subcultured and identified as they appeared. Isolation frequencies were calculated as the percentage of the 125 plates of each type colonized by each fungus. Frequencies for the four most common genera are shown in Table 6.1.

Six species of *Oidiodendron* Robak (*O. griseum* Robak, *O. maius* Barron, *O. periconioides* Morrall, *O. rhodogenum* Robak, and two unidentified species, *Oidiodendron* sp. 1 and 2), numerous isolates of the *Geomyces pannorum* (Link) Sigler & Carmichael complex, and two new species of *Pseudogymnoascus* Raillo [*P. appendiculatus* Rice & Currah and *P. verrucosus* Rice & Currah (chapter 5)] were isolated from the bait blocks. Ten isolates of *G. pannorum*, four each of *P. appendiculatus* and *Oidiodendron* sp. 1, three each of *O. maius* and *O. rhodogenum*, two each of *P. verrucosus* and *O. periconioides*, and one isolate each of *O. griseum* and *Oidiodendron* sp. 2 were used in the enzyme assays and the mass-loss study. One isolate each of *Bjerkandera adusta* and *Phanerochaete chrysosporium*, from the University of Alberta Microfungus Collection and Herbarium (UAMH), were used for comparison. Cultures are deposited at UAMH or maintained by the author at the Department of Biological Sciences, University of Alberta.

6.2.2. *Enzyme Assays*

Three replicates of each isolate were used in the enzyme assays. Cultures were inoculated using mycelial plugs 1 cm in diameter and incubated at 15°C in the dark for four weeks unless otherwise stated.

The cellulose azure method (Smith 1977, Rice & Currah 2001) was used to assay cellulolytic ability. Briefly, 10 ml modified Melin-Norkrans agar [MMN; 12.0 g Bacto agar (Becton Dickinson Co.), 3.0 g Difco malt extract (Becton Dickinson Co.), 1.0 g d-glucose anhydrous, 0.5 g NaCl, 10.0 g KH_2PO_4, 5.0 g $(NH_4)_2HPO_4$, 3.0 g $MgSO_4 \cdot 7H_2O$] was added to 20-ml vials as a basal medium, autoclaved, and allowed to solidify. A 2% (w/v) solution of cellulose azure (Sigma Chemical Co.) in MMN was autoclaved and 1 ml pipetted into each vial. Vials were scored based on the release of dye, through cellulose digestion, into the basal medium.

The ability to degrade phenolic compounds was tested using tannic acid medium (TAM) (Bending & Read 1997, Rice & Currah 2001), wood guaiacol medium (WDG) (Miyamoto *et al.* 2000, Rice & Currah, in press 1) and an analogous *Sphagnum* guaiacol medium (SG). Mycelial plugs were placed on TAM [5.0 g tannic acid (BDH Laboratories, Poole, UK), 200 ml dH_2O combined with 15.0 g Difco malt extract, 20.0 g Bacto agar, 800 ml dH_2O after autoclaving] and incubated for 48 hours. Darkening of the medium under the plug indicates degradation of soluble phenolic polymers (Bending & Read 1997). Mycelial plugs were placed on WDG [2.0 g spruce wood powder (collected locally), 18.0 g Bacto agar, 1.0 l dH_2O, 100 μl guaiacol (Sigma Chemical Co.) added after autoclaving] and SG [2.0 g ground *Sphagnum fuscum* (collected from Perryvale Bog), 18.0 g Bacto agar, 1.0 l dH_2O, 100 μl guaiacol added after autoclaving] and scored based on the red discoloration that indicates degradation of insoluble phenolic polymers (Miyamoto *et al.* 2000), including lignin (WDG) and *Sphagnum*-specific polymers (SG).

6.2.3. *Mass Loss Studies*

For each of three replicates per isolate, a 3 x 3 cm 63 μm gauge polyester pouch containing 0.05 to 0.10 g of *Sphagnum fuscum* was placed on water agar (WA; 20.0 g Bacto agar, 1.0 l dH_2O), inoculated with a 1 cm diameter mycelial plug, and incubated at 15°C in the dark for 16 weeks. Three uninoculated controls allowed the measurement of mass loss due to leaching. Each pouch, containing the top 3 cm of three healthy looking *Sphagnum fuscum* plants, was dried at 50°C, weighed to the nearest 0.001 g, autoclaved at 121°C for 20 minutes (liquid cycle) and then placed in a Petri plate. After 16 weeks, pouches were dried at 50°C to a constant weight, and the mass loss of each calculated by subtracting the final weight from the initial weight. The average mass loss of control pouches was subtracted from that value. Mass losses were expressed as a percentage of the initial mass.

6.2.4. *SEM Observations*

One isolate each of *Geomyces pannorum, Pseudogymnoascus appendiculatus, P. verrucosus, Oidiodendron maius, O. periconioides, Oidiodendron* sp. 2, *Bjerkandera adusta*, and *Phanerochaete chrysosporium* was used for SEM examination. For each isolate, the top 5 mm was removed from one of the plants used in the mass loss study and prepared for SEM examination using a tannic acid-guanidine hydrochloride and osmium fixation method (Tsuneda *et al.* 1991, 2001). Samples were immersed in phosphate buffer (pH 7; VWR Scientific Products, West Chester, PA) under a weak vacuum, fixed in 2% glutaraldehyde (Fisher Scientific, Fair Lawn, NJ) for four hours at room temperature, and immersed in a 2% tannic acid-2% guanidine hydrochloride (JT Baker Inc., Phillipsburg, NJ) solution overnight at 5°C. Samples were rinsed in dH_2O and postfixed in 2% OsO_4 (Sigma Chemical Co.) for three hours at room temperature, rinsed in dH_2O, and dehydrated using an ethanol series (25, 50, 75, 90, 95, 100%) with three changes of each at thirty minute intervals. Samples were placed in 50% amylacetate (Aldrich Chemical Co., Milwaukee, WI) (in ethanol) and then 100% amylacetate before being critical point dried in Teflon capsules. Samples were coated with cold and the leaf cells observed and photographed using a Hitachi S-510 SEM (Hitachi Science Systems, Japan).

6.3. Results

The four most common genera of filamentous fungi isolated from the bait blocks were *Geomyces, Penicillium* Link, *Mucor* Fresenius, and *Oidiodendron* (Table 6.1). *Geomyces* was the most commonly observed genus in moist chambers and MYCO plates while *Mucor* was the most common on CMAB (Table 6.1). *Penicillium* species were observed on about half of all plates. *Oidiodendron* species were found on over half of the moist chambers but on less than one percent of the agar plates.

All species, except *Oidiodendron* sp. 1, degraded cellulose azure (Table 6.2). The tannic acid assay for the degradation of soluble phenolics gave variable results with *O. griseum, O. maius, O. periconioides, Oidiodendron* sp. 1, and *P. verrucosus* testing positive and *O. rhodogenum, Oidiodendron* sp. 2, and *P. appendiculatus* negative. Isolates of *G. pannorum* varied in their TAM reaction: seven were negative and three positive. Neither basidiomycete showed a positive TAM reaction (Table 6.2). In contrast, none of the *Myxotrichaceae* degraded insoluble phenolics, as indicated by negative reactions on SG and WDG, while both basidiomycetes were positive on both media (Table 6.2).

Mass losses ranged from negligible (*B. adusta* and individual isolates of *G. pannorum, O. maius*, and *Oidiodendron* sp. 1) to approximately 50% (*O. periconioides*) with most species causing average mass losses of approximately 15% (Table 6.2). Variation was high among replicates and conspecific isolates, with standard deviations ranging from 1 to almost 50% (Table 6.2). For example, isolates of *G. pannorum* caused mass losses ranging from –3 to 41% and isolates of *O. maius* caused mass losses ranging from –2 to 47% (Table 6.2). Mean mass losses caused by most *Myxotrichaceae* were intermediate between those caused by *B. adusta* (-2%) and *Ph. chrysosporium* (37%).

SEM observations showed that all species grew and sporulated on the *Sphagnum*, and eroded the walls of the hyaline cells. Cell wall erosion was not uniform; some areas of the leaves remained intact while others were completely eroded. Two decay patterns were observed with the *Myxotrichaceae* causing a pattern that resembled "simultaneous white rot" while the basidiomycetes caused a form of "preferential white rot".

The six *Myxotrichaceae* (Figure 6.1) grew and sporulated abundantly (A-E) on areas that varied in decay stage from little cell wall erosion (A) to advanced decay characterized by voids (D, E). Characteristic conidia (asexual spores) and associated structures often developed on areas of cell wall erosion (B-E, H, I). Hyphae penetrated cell walls (F) or grew through pores (G) then grew both on the surface and inside the cells (D, F-I). In early stages of decay, the cell walls show slight wavy deformations and puckering (C, F, G), particularly in areas near cell wall thickenings (F), or more pronounced deformations of the cells (B, H). Thinning of the cell wall (C, H) and the formation of localized voids (C-E, I) follow as cell walls are eroded. The voids increased in size as decay progressed (E, I) and different stages of decay were observed in close proximity (C, H). All cell wall erosion occurred adjacent to viable (D, F-I) or autolyzing (C, D, G-I) hyphae or conidia and conidiophores (B-F).

Both basidiomycetes (Figure 6.2) grew and sporulated more sparsely on the *Sphagnum* (A-D) than the *Myxotrichaceae* with growth and conidial production more concentrated in areas where cell wall deformation or erosion was visible (B-D). Hyphae penetrated the cell walls (E, F) or entered the cells through pores (F) and grew on the outer surfaces (E-G) and inside the cells (H, I). Pronounced cell deformation (B, D) occurred in early decomposition and was followed by the gradual exposure of the cellulose microfibrils. Initial exposure of the microfibrils gave the cells a stringy and rough appearance (D), which was followed by the exposure of the net-like cellulose matrix (H-J). In some cases, the cellulose was also degraded, producing voids (G). Most cell wall erosion occurred close to viable or autolyzing hyphae (G-J) but it was not restricted to areas immediately adjacent to the hyphae (G, H).

6.4. Discussion

Carbon storage in peatlands occurs because of the slow decomposition of peat; particularly *Sphagnum* remains (Clymo 1965, Gorham 1991, Vitt 1994, Verhoeven & Liefveld 1997, Limpens & Berendse 2003). Studies have shown that *Sphagnum* decomposes slowly *in situ* (e.g. Clymo 1965, Verhoeven & Liefveld 1997, Thormann *et al.* 2001a, Limpens & Berendse 2003) and *in vitro* (Verhoeven & Liefveld 1997, Thormann *et al.* 2002, 2004a) and have suggested that this is due both to the chemical composition of the *Sphagnum* remains and the environmental conditions in bogs. The interactions among these factors and their effects on decomposer microbes and decomposition dynamics are not well understood (e.g. Thormann *et al.* 2004a) and more studies are needed to determine how each of the environmental and chemical factors affect decomposers and how they interact to determine decomposition dynamics in peatlands. The abundance of polyphenolic compounds in *Sphagnum* cell walls and peat, high carbon to nitrogen ratios, and low nutrient status have been provided as explanations of the slow decomposition of *Sphagnum* peat. However, wood is also high in phenolic compounds, has a high carbon to nitrogen ratio, and low nutrient concentrations but Thormann *et al.* (2002) found that mass losses were higher for spruce wood (3-10% over eight weeks) than for *Sphagnum* (0-5% over eight weeks) although some species, including *Oidiodendron chlamydosporicum* Morrall, caused similar mass losses of both substrates. Thus, additional factors, for example, the presence of inhibitory or antibiotic compounds in *Sphagnum*, are necessary to explain the slower decomposition of *Sphagnum* relative to wood (Verhoeven & Liefveld 1997, Thormann *et al.* 2002). The identity and activity of these compounds could be determined *in vitro* and their effects assayed *in situ*.

Wood decay has been studied more frequently than the decay of *Sphagnum* (e.g. Tsuneda *et al.* 1991, Blanchette 1995, Reid 1995, Yatskov *et al.* 2003, Ganjegunte *et al.* 2004) and the molecular and biochemical processes involved in wood decay are relatively well understood (Tsuneda *et al.* 1991, Blanchette 1995, Reid 1995, Higuchi *et al.* 2004, Ludwig *et al.* 2004). The discovery that *Sphagnum* decay occurs in an analogous fashion to white rot of wood suggests that wood decay could be used as a model to predict and explain processes involved in *Sphagnum* decomposition. The continuing slow decomposition of *Sphagnum* remains is critical for the long term storage of carbon in peatlands but it has been suggested that decomposition of this material will increase dramatically under warmer, dryer conditions caused by global warming (e.g. Gorham 1991, Hogg *et al.* 1992, Roulet 2000, Freeman *et al.* 2001). However, there is very little empirical evidence to support or refute that hypothesis. Hogg *et al.* (1992) found that increased temperatures led to increased *in vitro* decomposition of *Sphagnum*-dominated peat only when drying occurred concomitantly. Thormann *et al.* (2004a) found that increased temperatures did not uniformly lead to increased mass losses of *Sphagnum fuscum* by suites of bacteria and fungi. On average, the mass losses I observed (mean approximately 15%) were higher than those observed by Thormann *et al.* (2002, 2004a) (typically less than 5%) even though my experiment was conducted at a lower temperature. Unfortunately, the longer incubation period and use of different fungal isolates and species do not allow comparison with the earlier works with regards to temperature. Further comparative studies of the decomposition of *Sphagnum* and wood could be combined with available information on rates of wood decay under different temperature and moisture conditions as well as information on rate-limiting factors, like carbon to nitrogen ratios, to provide more accurate predictions about the rates of *Sphagnum* decay under different climate change scenarios.

A wide variety of microfungi have been isolated from the *Sphagnum* peat in Perryvale Bog (e.g. Tsuneda *et al.* 2000, Thormann *et al.* 2001b, 2004b, Rice & Currah 2002, Thormann, in press 1,2, chapter 5) and are likely the primary decomposers responsible for releasing carbon and nutrients stored in the peat (see Thormann, in press 1,2). Among these fungi, cellulolytic activity is more common than the degradation of polyphenolic polymers, with about half of the fungi reported from Perryvale Bog being cellulolytic while less than one quarter degraded polyphenolic polymers (Thormann *et al.* 2001b, 2002). In most studies of peatland fungi (see Thormann, in press 1 for a review), ubiquitous, fast-growing, prolific-sporulating fungi, including species of *Penicillium* and *Mucor*, have been the most common fungi reported from peat. These genera include the most common species reported from peat samples from Perryvale Bog (Thormann *et al.* 2001b, 2004b, Rice & Currah 2002) and they were also among the most common taxa recovered from bait blocks (Table 6.1). While these fungi are probably playing important roles in decomposition, they are likely over-represented due to their prolific sporulation and rapid growth on standard culture media, as evidenced by their relative scarcity on moist incubated peat (Rice & Currah 2002). *Penicillium* species produce a variety of enzymes (e.g. Domsch *et al.* 1980) and are likely degrading simple and complex polymers in the peat (see Thormann, in press 2 for discussion). Mucoralean fungi have a preference for simple sugars (e.g. Domsch *et al.* 1980) and likely play a role in the initial decomposition of senescent material and may also degrade the byproducts of the decomposition of more complex material (see Thormann, in press 2).

Species of *Myxotrichaceae* are also common in peat (Barron 1962, Schild *et al.* 1988, Sigler & Flis 1998, Thormann *et al.* 2001b, 2004b, Rice & Currah 2002, in prep, Thormann, in press 1, Table 6.1) and degrade a variety of simple and complex polymers, including cellulose (Currah 1985, Dalpé 1991, Udagawa *et al.* 1993, Uchiyama *et al.* 1995, Sigler *et al.* 2000, Rice & Currah 2001, in press 1, Thormann *et al.* 2002, Table 6.2), some phenolic polymers (Rice & Currah 2001, in press 1, Thormann *et al.* 2002, Table 6.2), pectin, starch, gelatin, lipids, chitin, (e.g. Bending & Read 1996, 1997, Rice & Currah 2001, in press 1, Thormann *et al.* 2002). Notably, the two *Myxotrichaceae* (*Oidiodendron maius* and *O. chlamydosporicum*) isolated from Perryvale Bog by Thormann *et al.* (2001b, 2002) degraded both cellulose and soluble phenolics, as did six of the nine species included in my study (Table 6.2), while the other three species degraded either cellulose or soluble phenolics. These abilities occurred in all three genera of *Myxotrichaceae* included in the study, suggesting that these enzymatic activities may be widespread in the family and may contribute to their success as saprobes in peat, as well as wood and soil. Negative reactions on the SG and WDG media may indicate either an inability to degrade insoluble phenolics or inhibition of the fungi by guaiacol.

Oidiodendron maius, a species commonly considered an ericoid mycorrhizal symbiont of ericaceous shrubs (e.g. Douglas *et al.* 1989, Perotto *et al.* 1995, Hambleton & Currah 1997, Rice & Currah, in press 2) rather than a saprobe has previously been shown to decompose *Sphagnum* (Tsuneda *et al.* 2001, Piercey *et al.* 2002, Thormann *et al.* 2002), as has the saprobic *O. chlamydosporicum* (Thormann *et al.* 2002). The mass losses of *Sphagnum* caused by *O. maius* in previous studies ranged from 1.5-2.5% (Thormann *et al.* 2002) to 10-15% (Piercey *et al.* 2002). These values are comparable to those obtained for two of my isolates but much lower than the value I observed for the third isolate of *O. maius* (almost 50%) (Table 6.2), suggesting that the differences may be due more to strain-specific effects than to differences in experimental design. My results also indicate that other *Myxotrichaceae* can cause mass losses of *Sphagnum*, some to a greater extent than *O. maius* or *O. chlamydosporicum*, and that they all decay the walls of hyaline cells in the same way. This pattern, which resembles simultaneous white rot of wood, had previously been observed only in *O. maius* (Tsuneda *et al.* 2001). The consistency of these findings, coupled with the acidophilic nature of many of these species (Rice & Currah, in press 1) and their abundance in peat, suggests that most *Myxotrichaceae* have the potential to degrade *Sphagnum* as well as wood and that they may be important saprobes in peatlands. Peatlands are nutrient poor ecosystems because their nutrients are sequestered in plant remains in the peat. In bogs, since those remains are primarily *Sphagnum*, nutrient release from the decomposition of these mosses is critical to nutrient cycling and productivity. The ability of some *Myxotrichaceae* to form ericoid (e.g. Couture *et al.* 1983, Dalpé 1986, 1989, 1991, Douglas *et al.* 1989, Perotto *et al.* 1995, Hambleton & Currah 1997, Sigler & Flis 1998, Rice & Currah, in press 2) and possibly ectomycorrhizal (Perotto *et al.* 1995, Sigler & Flis 1998, Bergero *et al.* 2000) associations with the dominant vascular plants in bogs may contribute further to their importance in nutrient cycling (Rice & Currah, in press 2) since the nutrients they release by decomposing *Sphagnum* could be provided directly to their host plants (Northup *et al.* 1995, Aerts 2002, Leake *et al.* 2002), possibly enhancing host plant productivity.

Basidiomycetes are rarely reported in surveys of microfungi in peatlands (e.g. Thormann *et al.* 2001b, Thormann, in press 1, 2) and represented less than 1% of my isolates. Yet basidiomycetes, especially wood decay basidiomycetes, are important decomposers of lignocellulose debris, including wood and leaf and needle litter, in many environments (e.g. Tsuneda *et al.* 1991, Blanchette 1995, Reid 1995, Domisch *et al.* 2000, Miyamoto *et al.* 2000, Osono & Takeda 2002, Yatskov *et al.* 2003, Ganjegunte *et al.* 2004). Cellulolytic and phenol-degrading activities are well-known in white-rot basidiomycetes (e.g. Blanchette 1995, Reid 1995, Higuchi 2004, Ludwig *et al.* 2004), as is the degradation of other polyphenolic and aromatic compounds (e.g. Mai *et al.* 2004, Walter *et al.* 2004), and my study adds *Sphagnum*-specific polyphenolics to the list. My results also show that white-rot basidiomycetes are proficient decomposers of *Sphagnum* under laboratory conditions, causing a pattern of preferential white rot. These results suggest either that most basidiomycetes are excluded from peat for some other reason, such as the presence of inhibitory compounds, or that they are underestimated in fungal sampling. Mushrooms have been observed growing among *Sphagnum* plants in Perryvale Bog (Thormann *et al.* 2001b, Rice, unpublished) and wood decay fungi grow on trees and decaying wood in the bog and adjacent uplands (personal observations). Once buried in the peat, however, wood decomposes slowly and remains recognizable for many years, suggesting that, beneath the surface, activity of wood decay fungi could be low. Additional surveys combining selective isolations and culture-free methods (e.g. environmental PCR) are needed to determine the relative frequency of white-rot basidiomycetes in bogs.

My hypothesis that ascomycetes (i.e. *Myxotrichaceae*) would display a soft rot pattern of decay where the middle layer of the *Sphagnum* cell wall was left intact was unsupported. Both the ascomycetes and basidiomycetes demonstrated patterns of decay of hyaline cells that resembled white rot of wood. However, the ascomycetes differed because they removed all cell wall components more or less simultaneously to produce localized voids that increased in size as decomposition progressed (Figure 6.1; "simultaneous white rot") while the basidiomycetes preferentially removed the polyphenolic matrix, gradually exposing greater areas of the cellulose microfibrils, before eventually producing voids (Figure 6.2; "preferential white rot") (Blanchette 1995, Reid 1995). In a previous study (Tsuneda *et al.* 2001), another ascomycete (*Pochonia bulbillosa* = "*Acremonium* cf. *curvulum*) showed a preferential white rot pattern similar to the one I observed for the two basidiomycetes, except that decay was restricted to areas adjacent to the hyphae. The ability of ascomycetes to remove phenolic polymers from *Sphagnum*, but not wood, may be due to the different suites of monomers comprising the polyphenolics in *Sphagnum* cell walls. Notably, the decay caused by the ascomycetes is restricted to areas adjacent to the hyphae and, thus, unlike that caused by the basidiomycetes, is not likely due to the diffusion of enzymes within the substrate. This suggests that degradation of *Sphagnum* may be limited by the rate of growth through the substrate. The high mass losses of *Sphagnum* caused by ascomycetes contrasts with the pattern observed in deciduous leaf litters (Osono & Takeda 2002), in which, wood decay basidiomycetes caused much higher mass losses than most ascomycetes; the exception being members of the *Xylariaceae*, an ascomycete family that causes a form of white rot of wood and caused mass losses of leaf litter comparable to those caused by white-rot basidiomycetes (Osono & Takeda 2002).

Mass loss values were not well correlated with the amount of cell wall degradation observed by SEM. SEM examination of species that caused different percent mass losses revealed similar amounts of cell wall erosion while species causing similar mass losses caused different levels of cell wall erosion. For example, *B. adusta* caused negligible mass loss while *Ph. chrysosporium* caused mean mass losses over 30% but the two species eroded the cell walls to approximately the same extent. The two species of *Pseudogymnoascus* caused similar mean mass losses (approximately 15%) but much more cell wall erosion was observed on leaves degraded by *P. appendiculatus* than on leaves degraded by *P. verrucosus*. *Oidiodendron periconioides* caused the highest mean mass losses (approximately 50%) but other species, including *G. pannorum*, eroded the leaf cell walls to a similar, if not greater, extent. Some of these discrepancies could be explained by differential mass losses from different parts of the plants. Also, small fragments from the tops of the plants were examined using SEM and cell wall erosion might have occurred at different rates on different parts of the plants; erosion was patchy, even on single leaves. Differential mass losses may have also occurred from stems, which were not examined, and from the cytoplasm of green cells and other living cells. Also mass loss values did not account for increases in fungal biomass since fungal mycelium could not be removed from the *Sphagnum* leaves before the final weighing. Differences in fungal growth and biomass accumulation may account for some of the observed discrepancies in mass loss and cell wall erosion, with fungal strains that accumulated more biomass showing less mass loss but more cell wall erosion. The accumulation of fungal biomass also explains the negative mass loss values observed for some isolates where the mass gained by the fungal mycelium was greater than the mass lost from the *Sphagnum* due to carbon or water uptake from the agar plug or basal medium. These discrepancies suggest that mass loss is not entirely attributable to the decomposition of the cell walls and that each of the two methods for assessing decomposition provides only partial information about the potential of fungi to degrade *Sphagnum*. The two methods should be used to provide complimentary information about the mode of attack and amount of decay to provide as complete of a picture as possible of the possible roles of fungi in nature. The discrepancies between mass loss and erosion data could be reduced in future studies by correcting for fungal biomass and by observing larger areas and different portions of the plant, including the stems and lower branch leaves to determine the rate at which these parts decompose. The discrepancies between the mass loss values I observed and those observed in previous studies (Piercey *et al.* 2002, Thormann *et al.* 2002, 2004a) should also be investigated. While some species in each study caused negligible mass losses of *Sphagnum*, the upper limits of mass loss were much higher in my study and this discrepancy cannot be explained entirely by strain-specific effects, or different incubation temperatures or periods.

Additional research is necessary to improve understanding of decomposer fungi and decomposition dynamics in peatlands. *In vitro* studies can suggest the potential roles of individual fungal species or consortia but cannot replicate the complexity of natural ecosystems so extrapolation is risky. Meanwhile, cultural surveys and environmental PCR can indicate taxonomic diversity and richness of the community but cannot provide information regarding the ecological roles and interactions among individual species. The roles of individual species or assemblages are difficult or impossible to elucidate from *in situ* studies of ecological processes. Therefore, *in vitro* assessments of the potential roles of individual species must be coupled with surveys of taxonomic diversity and *in situ* quantification of ecological processes, such as decomposition rates and nutrient transfer via mycorrhizal connections, in order to understand the roles of fungi in ecological processes and predict their responses to environmental disturbances.

Table 6.1. Observational frequencies (% of 125 plates colonized) of the four most frequently recovered genera from lignin-rich bait blocks placed in Perryvale Bog.

Genus	Moist Chamber	CMAB	MYCO
Geomyces[a]	85.6	33.6	81.6
Penicillium	78.4	36.0	25.6
Mucor	45.6	56.0	28.8
Oidiodendron	56.0	0.1	0.1

CMAB = Cornmeal agar + benomyl, MYCO = mycosel agar

[a] Includes the anamorphs of *Pseudogymnoascus* species

Table 6.2. Enzyme assay results (+/-) and percentage mass loss of *Sphagnum* [mean (standard deviation)] for *Geomyces pannorum*, six *Oidiodendron* species, two *Pseudogymnoascus* species, *Bjerkandera adusta*, and *Phanerochaete chrysosporium*.

Species	Strain	CEL	TAM	SG	WDG	Mass Loss
Geomyces pannorum	2MMC1-3A	+	-	-	-	15.9 (6.1)
	3MM1-5	+	-	-	-	40.7 (27.0)
	1JnB1-2B	+	+	-	-	27.0 (29.0)
	4JnB2-1B	+	+	-	-	13.9 (21.2)
	2JyM4-2	+	-	-	-	-3.1 (7.4)
	5JyB2-2	+	-	-	-	13.6 (6.9)
	3AMC4-2	+	-	-	-	11.6 (8.4)
	4AMC2-1	+	-	-	-	6.2 (16.7)
	1SMC2-1	+	+	-	-	8.9 (6.1)
	5SM1-5	+	-	-	-	0.8 (15.5)
Oidiodendron griseum	3MMC3-4A	+	+	-	-	6.4 (8.4)
O. maius	5MMC3-6	+	+	-	-	47.2 (32.7)
	3JyMC4-2C	+	+	-	-	-2.1 (8.0)
	2AMC4-2	+	+	-	-	11.7 (19.5)
O. periconioides	UAMH 10463	+	+	-	-	44.9 (21.0)
	UAMH 10522	+	+	-	-	55.5 (18.2)
O. rhodogenum	3MMC1-8A	+	+	-	-	37.2 (26.8)
	UAMH 10462	+	+	-	-	8.6 (1.5)
	UAMH 10521	+	+	-	-	17.4 (24.4)
Oidiodendron sp. 1	3MMC3-7A	-	+	-	-	24.0 (26.5)
	5JyMC2-5A	-	+	-	-	-4.9 (3.5)
	2SMC1-1B	-	+	-	-	21.4 (22.0)
	2SMC5-1A	-	+	-	-	3.9 (9.3)
Oidiodendron sp. 2	4SM3-3	+	-	-	-	29.0 (20.9)
Pseudogymnoascus appendiculatus	3JyM3-1	+	-	-	-	2.8 (48.4)
	UAMH 10510	+	-	-	-	18.5 (14.2)
	UAMH 10511	+	-	-	-	19.1 (16.4)
	UAMH 10512	+	-	-	-	21.9 (26.8)
P. verrucosus	UAMH 10579	+	+	-	-	23.3 (1.2)

	UAMH 10580	+	+	-	-	8.2 (5.4)
Bjerkandera adusta	UAMH 8528	+	-	+	+	-2.0 (10.8)
Phanerochaete chrysosporium	UAMH 4521	+	-	+	+	36.6 (4.4)

CEL = Cellulose azure, TAM = tannic acid medium, SG = *Sphagnum* guaiacol medium, WDG = wood guaiacol medium

Figure 6.1. Degradation of *Sphagnum* leaves by species of *Myxotrichaceae*. Pattern of decay resembles simultaneous white-rot of wood.

A. *Oidiodendron maius* growing and sporulating on *Sphagnum* leaves, erosion of the cell walls is not readily apparent. Bar = 100 µm. **B**. Asexual spores (conidia, C) and spore bearing structures (conidiophores, arrow) of *O. maius* associated with deformed areas of a leaf (arrowhead). Bar = 50 µm. **C**. Conidia (C) of *Pseudogymnoascus appendiculatus* adjacent to a degraded area (arrows). Various stages of decay occur in close proximity to autolyzed hyphae (A): wavy deformations (arrowheads), thinning of the cell wall (T), and localized voids (V). Bar = 5 µm. **D**. Degraded area with voids (arrows) where the cell wall has been completely eroded and thin areas where fragments of the cell wall remain (arrowheads). Erosion is restricted to areas adjacent to hyphae (H) and conidia (C) of *Geomyces pannorus*. Bar = 10 µm. **E**. Variable erosion by *G. pannorus*; areas where the cell wall has been almost eroded (E) are next to intact areas (I). Bar = 10 µm. **F**. Hyphae of *P. verrucosus* penetrate the cell wall (arrows) near small patches of erosion (E) and wavy deformations (arrowheads). Bar = 1.25 µm. **G**. Hyphae (H) of *O. periconioides* growing into pores (P) of hyaline cells. The cell wall is eroded between the pores and near autolyzing hyphae (A). Bar = 5 µm. **H**. Eroded (E) and distorted (D) portions of a leaf adjacent to hyphae (H) and conidiophores (C) of *O. periconioides*. Bar = 40 µm. **I**. Hyphae of *G. pannorus* criss-crossing an eroded portion of the leaf with adjacent voids and thin patches. Bar = 5 µm.

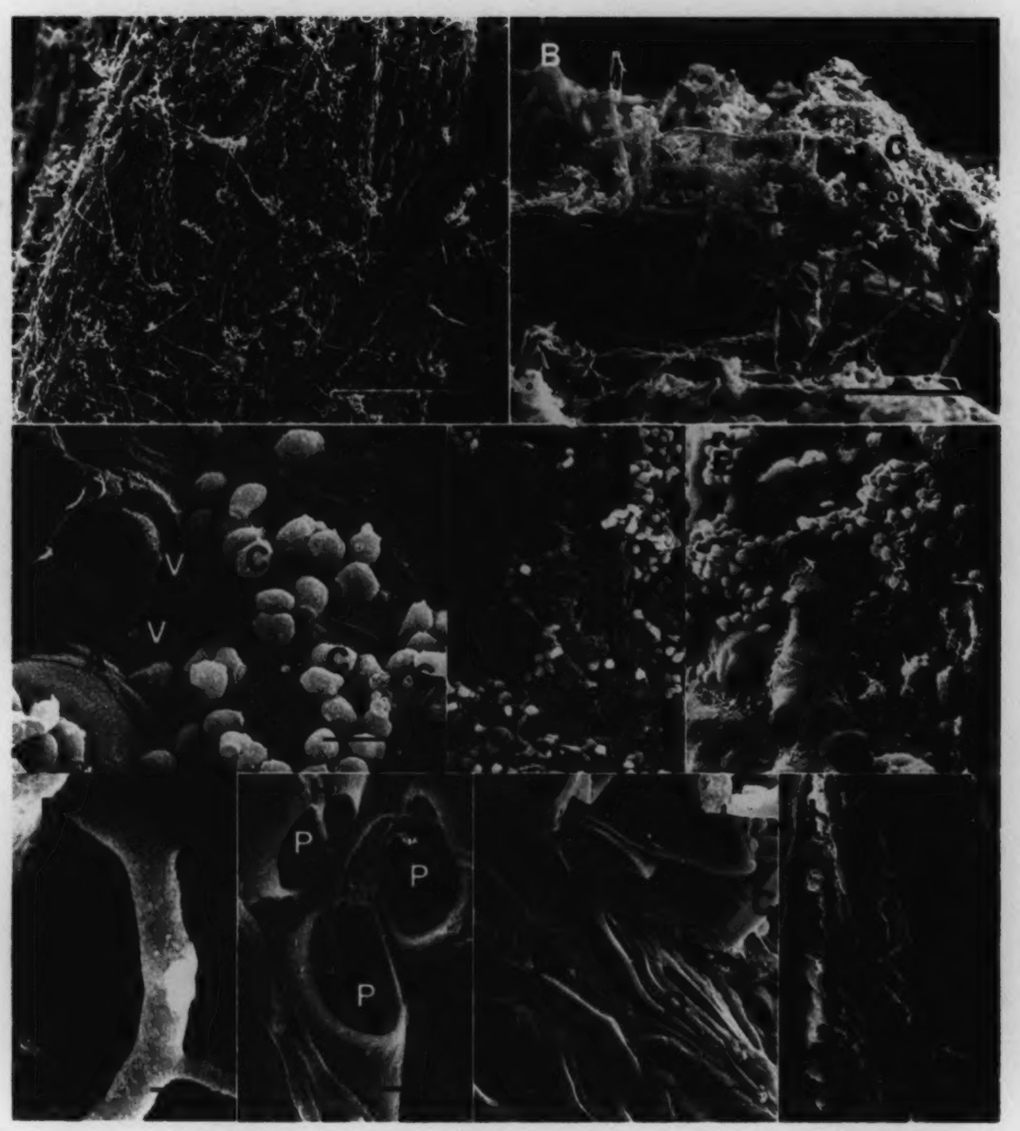
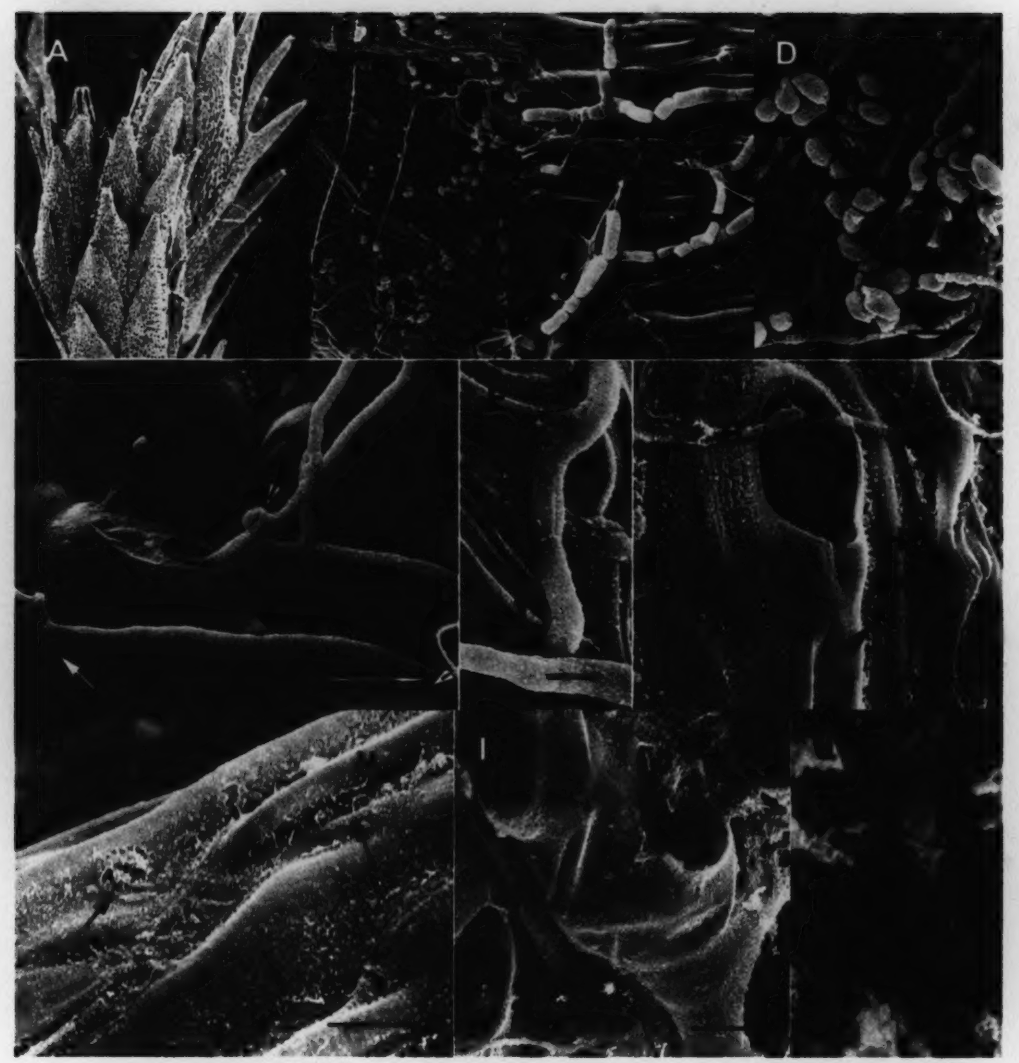

B
C
V
C
V
C
E
P
P
P

Figure 6.2. Degradation of *Sphagnum* leaves by two white-rot basidiomycetes, *Bjerkandera adusta* and *Phanerochaete chrysosporium*. Pattern of decay resembles preferential white-rot of wood.

A. Hyphae of *Ph. chrysosporium* growing on *Sphagnum* leaves. Bar = 250 µm. **B**. *Ph. chrysosporium* hyphae and conidia on distorted (D) portions of a leaf. Bar = 12.5 µm. **C**. Conidia of *B. adusta* on an intact portion of a leaf. Bar = 10 µm. **D**. Conidia (C) of *Ph. chrysosporium* on a leaf. Exposure of cellulose microfibrils gives cells a stringy appearance (arrows). Bar = 10 µm. **E**. Hyphae of *B. adusta* growing into pores of a hyaline cell and penetrating the cell wall (arrow). Clamp connections (arrowheads) are formed along the hyphae. Bar = 10 µm. **F**. Hyphae of *Ph. chrysosporium* penetrating (arrows) distorted portions of a leaf. Bar = 5 µm. **G**. Erosion of the amorphous material of the cell wall exposes a net-like matrix of cellulose microfibrils (arrows) and localized voids (arrowhead) where the cellulose fibrils are eroded. Erosion occurs up to 20 µm from hyphae (H) of *Ph. chrysosporium*. Bar = 5 µm. **H**. Net-like pattern of exposed cellulose microfibrils (arrows) extends more than 10 µm from hyphae (H) of *Ph. chrysosporium*. Bar = 5 µm. **I**. Erosion (E) of the cell walls near pores. A hypha (H) of *B. adusta* passes near one patch. Bar = 5 µm. **J**. Exposed cellulose microfibrils (E) and localized voids (arrows) near a conidium (C) of *B. adusta*. Bar = 2.5 µm.


A
D
I

6.5. Literature Cited

Aerts R (2002). The role of various types of mycorrhizal fungi in nutrient cycling and plant competition. In: van der Heijden MGA, Sanders IR (eds) *Ecological Studies, vol 157. Mycorrhizal Ecology*. Springer-Verlag, Berlin. pp. 117–133.

Barron GL (1962). New species and new records of *Oidiodendron*. *Canadian Journal of Botany* **40**: 589–607.

Bending GD, Read DJ (1996). Nitrogen mobilization from tannin-protein complexes by ericoid and ectomycorrhizal fungi. *Soil Biology and Biochemistry* **28**: 1603–1612.

Bending GD, Read DJ (1997). Lignin and soluble phenolic degradation by ectomycorrhizal and ericoid mycorrhizal fungi. *Mycological Research* **101**: 1348–1354.

Bergero R, Perotto S, Girlanda MM, Vidano G, Luppi AM (2000). Ericoid mycorrhizal fungi are common root associates of a Mediterranean ectomycorrhizal plant (*Quercus ilex*). *Molecular Ecology* **9**: 1639–1649.

Blanchette RA (1995). Degradation of the lignocellulose complex in wood. *Canadian Journal of Botany* **73**: S999–S1010.

Clymo RS (1965). Experiments on the breakdown of *Sphagnum* in two bogs. *Journal of Ecology* **53**: 747–757.

Couture M, Fortin JA, Dalpé Y (1983). *Oidiodendron griseum* Robak: an endophyte of ericoid mycorrhiza in *Vaccinium* spp. *New Phytologist* **95**: 375–380.

Currah RS (1985). Taxonomy of the *Onygenales*: *Arthrodermataceae, Gymnoascaceae, Myxotrichaceae* and *Onygenaceae*. *Mycotaxon* **24**: 1–216.

Dalpé Y (1986). Axenic synthesis of ericoid mycorrhiza in *Vaccinium angustifolium* Ait. by *Oidiodendron* species. *New Phytologist* **103**: 391–396.

Dalpé Y (1989). Ericoid mycorrhizal fungi in the *Myxotrichaceae* and *Gymnoascaceae*. *New Phytologist* **113**: 523–527.

Dalpé Y (1991). Statut endomycorrhizien du genre *Oidiodendron*. *Canadian Journal of Botany* **69**: 1712–1714.

Domisch T, Finér L, Karsisto M, Laine J (2000). Decomposition of Scots pine litter and the fate of released carbon in pristine and drained pine mires. *Soil Biology and Biochemistry* **32**: 1571–1580.

Domsch KH, Gams W, Anderson T-H (1980). *Compendium of Soil Fungi*. Academic Press, United Kingdom.

Douglas GC, Heslin MC, Reid C (1989). Isolation of *Oidiodendron maius* from *Rhododendron* and ultrastructural characteristics of synthesized mycorrhizas. *Canadian Journal of Botany* **67**: 2206–2212.

Freeman C, Ostle N, Kang H (2001). An enzymatic 'latch' on a global carbon store. *Nature* **409**: 149.

Ganjegunte GK, Condron LM, Clinton PW, Davis MR, Mahieu N (2004). Decomposition and nutrient release from radiata pine (*Pinus radiata*) coarse woody debris. *Forest Ecology and Management* **187**: 197–211.

Gorham E (1991). Northern peatlands: role in the carbon cycle and probable responses to global warming. *Ecological Applications* **1**: 182–195.

Hambleton S, Currah RS (1997). Fungal endophytes from the roots of alpine and boreal *Ericaceae*. *Canadian Journal of Botany* **75**: 1570–1581.

Higuchi T (2004). Microbial degradation of lignin: Role of lignin peroxidase, manganese peroxidase, and laccase. *Proceedings of the Japan Academy. Series B. Physical and Biological Sciences* **80**: 204–214.

Hogg EH, Lieffers VJ, Wein RW (1992). Potential carbon losses from peat profiles: effects of temperature, drought cycles, and fire. *Ecological Applications* **2**: 298–306.

Leake JR, Donnelly DP, Boddy L (2002). Interactions between ecto-mycorrhizal and saprotrophic fungi. In: van der Heijden MGA, Sanders IR (eds) *Ecological Studies, vol 157. Mycorrhizal Ecology*. Springer-Verlag, Berlin. pp. 345–372.

Limpens J, Berendse F (2003). How litter quality affects mass loss and N loss from decomposing *Sphagnum*. *Oikos* **103**: 537–547.

Ludwig R, Salamon A, Varga J, Zamocky M, Peterbaur CK, Kulbe KD, Haltrich D (2004). Characterisation of cellobiose dehydrogenases from the white-rot fungi *Trametes pubescens* and *Trametes villosa*. *Applied Microbiology and Biotechnology* **64**: 213–222.

Lumley TC, Gignac LD, Currah RS (2001). Microfungus communities of white spruce and trembling aspen logs at different stages of decay in disturbed and undisturbed sites in the boreal mixedwood region of Alberta. *Canadian Journal of Botany* **79**: 76–92.

Mai C, Schormann W, Majcherczyk A, Huttermann A (2004). Degradation of acrylic copolymers by white-rot fungi. *Applied Microbiology and Biotechnology* **65**: 479–487.

Melin E, Nannfeldt JA (1934). Researches into the bluing of ground woodpulp. *Saertryck ur Svenska Skogsvårdsföreningens Tidskrift Hafte* **3-4**: 397–616.

Miyamoto T, Igarashi T, Takahashi K (2000). Lignin-degrading activity of litter-decomposing basidiomycetes from *Picea* forests of Hokkaido. *Mycoscience* **41**: 105–110.

Northup RR, Zengshou Y, Dahlgren RA, Vogt KA (1995). Polyphenol control of nitrogen release from pine litter. *Nature* **377**: 227–229.

Osono T, Takeda H (2002). Comparison of litter decomposing ability among diverse fungi in a cool temperate deciduous forest in Japan. *Mycologia* **94**: 421–427.

Perotto S, Perotto R, Faccio A, Schubert A, Varma A, Bonfante P (1995). Ericoid mycorrhizal fungi: cellular and molecular bases of their interactions with the host plant. *Canadian Journal of Botany* **73**: S557–S568.

Piercey MM, Thormann MN, Currah RS (2002). Saprobic characteristics of three fungal taxa from ericalean roots and their association with the roots of *Rhododendron groenlandicum* and *Picea mariana* in culture. *Mycorrhiza* **12**: 175–180.

Reid ID (1995). Biodegradation of lignin. *Canadian Journal of Botany* **73**: S1011–S1018.

Rice AV, Currah RS (2001). Physiological and morphological variation in *Oidiodendron maius*. *Mycotaxon* **79**: 383–396.

Rice AV, Currah RS (2002). New perspectives on the niche and holomorph of the myxotrichoid hyphomycete, *Oidiodendron maius*. *Mycological Research* **106**: 1463–1467.

Rice AV, Currah RS (in press 1). *Oidiodendron*: A survey of the named species and related anamorphs of *Myxotrichum*. *Studies in Mycology* (accepted Feb. 2005).

Rice AV, Currah RS (in press 2). *Oidiodendron maius*: Saprobe in *Sphagnum* peat, mutualist in ericaceous roots? In: Schulz B, Boyle C, Sieber T (eds) *Microbial Root Endophytes*. Springer-Verlag, Heidelberg (Accepted Jan. 2005).

Rice AV, Currah RS (in prep). Two new species of *Pseudogymnoascus* with *Geomyces* anamorphs their phylogenetic relationship with *Gymnostellatospora*.

Robak H (1932). Investigations regarding fungi on Norwegian ground woodpulp and fungal infections at woodpulp mills. *Saertrykk av Nyt Magazin for Naturvidenskaberne* **71**: 185–330.

Roulet NT (2000). Peatlands, carbon storage, greenhouse gases, and the Kyoto Protocol: prospects and significance for Canada. *Wetlands* **20**: 605–615.

Schild DE, Kennedy A, Stuart MR (1988). Isolation of symbiont and associated fungi from ectomycorrhizas of Sitka spruce. *European Journal of Forest Pathology* **18**: 51–61.

Schofield WB (2001). *Introduction to Bryology*. Blackburn Press, Caldwell, NJ, USA.

Sigler L, Flis A (1998). *Catalogue of the University of Alberta Microfungus Collections and Herbarium*, 3rd Edition. University of Alberta, Edmonton, AB, Canada. (available online at www.devonian.ualberta.ca/uamh)

Sigler L, Lumley TC, Currah RS (2000). New species and new records of saprophytic ascomycetes (*Myxotrichaceae*) from decaying logs in the boreal forest. *Mycoscience* **41**: 495–502.

Smith RE (1977). Rapid tube test for detecting fungal cellulase production. *Applied Environmental Microbiology* **33**: 980–981.

Thormann MN (in press 1). Diversity and function of fungi in peatlands: A carbon cycling perspective. *Canadian Journal of Soil Science*. (Accepted Mar. 2005).

Thormann MN (in press 2). The role of fungi in decomposition dynamics in peatlands. In: Vitt DH, Wieder RK (eds) *Boreal Peatlands*. Springer-Verlag, Berlin. (Accepted Mar. 2005).

Thormann MN, Bayley SE, Currah RS (2001a). Comparison of decomposition of belowground and aboveground plant litters in peatlands of boreal Alberta, Canada. *Canadian Journal of Botany* **79**: 9–22.

Thormann MN, Bayley SE, Currah RS (2004a). Microcosm tests of the effects of temperature and microbial species number on the decomposition of *Carex aquatilus* and *Sphagnum fuscum* litter from southern boreal peatlands. *Canadian Journal of Microbiology* **50**: 793–802.

Thormann MN, Currah RS, Bayley SE (1999). The mycorrhizal status of the dominant vegetation along a peatland gradient in southern boreal Alberta. *Wetlands* **19**: 438–450.

Thormann MN, Currah RS, Bayley SE (2001b). Microfungi isolated from *Sphagnum fuscum* from a southern boreal bog in Alberta. *The Bryologist* **104**: 548–559.

Thormann MN, Currah RS, Bayley SE (2002). The relative ability of fungi from *Sphagnum fuscum* to decompose selected carbon substrates. *Canadian Journal of Microbiology* **48**: 204–211.

Thormann MN, Currah RS, Bayley SE (2004b). Patterns of distribution of microfungi in decomposing bog and fen plants. *Canadian Journal of Botany* **82**: 710–720.

Tsuneda A, Maekawa N, Ohira I, Furukawa I (1991). Incipient decay of *Quercus serrata* sapwood by *Lentinus edodes* and its inhibition by an antagonistic hyphomycete, *Leptodontidium elatius*. *Canadian Journal of Botany* **69**: 2797–2825.

Tsuneda A, Thormann MN, Currah RS (2000). *Scleroconidioma*, a new genus of dematiaceous Hyphomycetes. *Canadian Journal of Botany* **78**: 1294–1298.

Tsuneda A, Thormann MN, Currah RS (2001). Modes of cell wall degradation of *Sphagnum fuscum* by *Acremonium* cf. *curvulum* and *Oidiodendron maius*. *Canadian Journal of Botany* **79**: 93–100.

Uchiyama S, Kamiya S, Udagawa S (1995). Five onygenalean fungi from Japan. *Mycoscience* **36**: 211–220.

Udagawa S, Uchiyama S (2000). Two onygenalean fungi from Russian Far East soil. *Mycoscience* **41**: 217–221.

Udagawa S, Uchiyama S, Kamiya S (1993). *Gymnostellatospora*, a new genus of the *Myxotrichaceae*. *Mycotaxon* **48**: 157–164.

Verhoeven JTA, Liefveld WM (1997). The ecological significance of organochemical compounds in *Sphagnum*. *Acta Botanica Neerlandica* **46**: 117–130.

Vitt DH (1994). An overview of the factors that influence the development of Canadian peatlands. *Memoirs of the Entomological Society of Canada* **169**: 7–20.

Walter M, Boul L, Chong R, Ford C (2004). Growth substrate selection and biodegradation of PCP by New Zealand white-rot fungi. *Journal of Environmental Management* **71**: 361–369.

Williams CJ, Yavitt JB (2003). Botanical composition of peat and degree of peat decomposition in three temperate peatlands. *Écoscience* **10**: 85–95.

Yatskov M, Harmon ME, Krankina ON (2003). A chronosequence of wood decomposition in the boreal forests of Russia. *Canadian Journal of Forest Research* **33**: 1211–1226.

CHAPTER 7: *OIDIODENDRON MAIUS*: SAPROBE IN *SPHAGNUM* PEAT, MUTUALIST IN ERICACEOUS ROOTS?[6]

7.1. Introduction

Oidiodendron maius Barron is a hyphomycete species isolated from peat, soil, decaying organic matter, and plant roots throughout temperate ecosystems, including peatlands, forests, and heathlands (e.g. Barron 1962, Nordgren *et al.* 1985, Schild *et al.* 1988, Hambleton & Currah 1997, Hambleton *et al.* 1998, Qian *et al.* 1998, Lumley *et al.* 2001, Thormann 2001, Thormann *et al.* 2001, 2004, Tsuneda *et al.* 2001, Rice & Currah 2002). The distribution of *O. maius* seems to parallel that of members of the *Ericaceae*, an angiosperm family that includes blueberries, cranberries, and rhododendrons, and which often dominates the vegetation in arctic and alpine meadows and temperate heathlands and the understory in boreal forests and peatlands (Hambleton 1998, Chambers *et al.* 2000, Hambleton & Currah 2000), and Mediterranean ecosystems (Perotto *et al.* 1995). This parallel distribution is probably based on a shared predilection for acidic, nutrient poor, organic soils, and perhaps also by a mycorrhizal association between *O. maius* and ericaceous plants. In the first instance, I can hypothesize that *O. maius* is a competitive and effective saprobe on acidic, organic soils because *O. maius* displays optimal growth in culture on acidic growth media (Rice & Currah 2001, in press), grows and sporulates readily on *Sphagnum* L. plants (Rice & Currah 2002), and has been shown *in vitro* to have the enzymatic ability to degrade the cell walls of *Sphagnum* leaves (Tsuneda *et al.* 2001). The role played by *O. maius* as a mycorrhizal associate of ericaceous shrubs is suggested first by its frequent isolation from ericaceous roots (e.g. Douglas *et al.* 1989, Perotto *et al.* 1995, 1996, Hambleton & Currah 1997, Currah *et al.* 1999, Monreal *et al.* 1999, Chambers *et al.* 2000, Johansson 2001, Usuki *et al.* 2003) and second by observations that it will form typical ericoid mycorrhizal infection units when reinoculated on *Ericaceae* grown in culture (e.g. Douglas *et al.* 1989, Xiao & Berch 1995, 1999, Monreal *et al.* 1999).

Since Douglas *et al.* (1989) described the ericoid mycorrhizas formed by *O. maius* in *Rhododendron* Chapman, most reports of *O. maius* have been from similar associations in other ericaceous plants. Its role in these associations has been considered one in which the plant derives some nutritional benefit (e.g. Perotto *et al.* 1995, 1996, Hambleton & Currah 1997, 2000, Johansson 2001). Oddly, the benefits accruing to the fungus in these relationships are rarely considered, possibly because they are considered secondary to the needs of the plant but perhaps also because they are difficult to determine (Douglas & Smith 1989). Unlike the arbuscular mycorrhizal fungi and many fastidious ectomycorrhizal basidiomycetes, *O. maius* does not have stringent requirements for host-derived sugars and growth factors and grows readily on many types of natural materials, including lichens, *Sphagnum*, and polypores, as well as on artificial growth media. In the absence of nutritional dependency, the benefits to the fungus in a mycorrhizal relationship are usually speculative. The relationship may provide the fungus with a carbon source, growth factors, habitat, a preemptive position as a consumer of senescent tissue, or a competitive advantage over other saprobes. Another explanation could be that the host plants are exploiting their fungal partners, a type of relationship well known in orchids where peloton-forming fungi are digested in mycorrhizal roots and germinating seeds where the fungus does not gain anything in return (Rasmussen 1995).

---

[6] A version of this chapter has been accepted for publication: Rice AV, Currah RS (in press) *Oidiodendron maius*: saprobe in sphagnum peat, mutualist in ericaceous roots? In: Schulz B, Boyle C, Sieber T (eds) *Microbial Root Endophytes*. Springer-Verlag, Heidelberg (Accepted Jan. 2005).

Thus, there are two possible explanations for the distribution of *O. maius*, i.e., it is a type of root endophyte, and possibly a mycorrhizal one, that requires its host plants to thrive in its habitats, and that it is a saprobe adapted to acidic conditions and enzymatically equipped to digest the intractable materials that accumulate in these areas. It is also possible that the species occupies both mycorrhizal and saprobic niches within suitable environments.

Acidic *Sphagnum* peatlands, found throughout the circumboreal region, are one ecosystem type that appears to support *O. maius* as both a saprobe and a root endophyte. These peatlands include bogs and fens with an understory of ericaceous shrubs, including *Rhododendron, Andromeda* L., and *Vaccinium* L. species and a thick ground layer of *Sphagnum* species (e.g. Vitt 1994, Svensson 1995, Vitt *et al.* 1996, Hoosbeek *et al.* 2001).

In Canada, many peatlands have a canopy of coniferous trees rooted in the *Sphagnum* (Vitt 1994, Vitt *et al.* 1996, Piercey *et al.* 2002). Bogs have a dense canopy of black spruce [*Picea mariana* (Miller) Britton, Sterns & Poggenburg] while poor fens are dominated by black spruce and larch (*Larix* Miller spp.) (Vitt 1994, Vitt *et al.* 1996). European peatlands tend to have open canopies with few trees, but, as in Canada, the common tree species in European peatlands are spruce [*Picea abies* (L) Karsten] and larch (*Larix* spp.) (e.g. Peteet *et al.* 1998). Ericoid mycorrhizal fungi, including *O. maius* have been isolated from ectomycorrhizal conifer roots (Summerbell 1987, Schild *et al.* 1988, Perotto *et al.* 1995, Qian *et al.* 1998, Bergero *et al.* 2000, Vrålstad *et al.* 2000), including the roots of sitka spruce in blanket bogs where *O. maius* was the most abundant sporulating species isolated from the roots (Schild *et al.* 1988). It has been proposed that, in peatlands, these fungi may form associations with the roots of coniferous canopy trees and ericaceous shrubs and also degrade the *Sphagnum* matrix (Piercey *et al.* 2002).

7.2. *Oidiodendron maius*

The hyphomycete genus *Oidiodendron* Robak was proposed by Robak in 1932 to accommodate three species (*O. fuscum* Robak, *O. nigrum* Robak, and *O. rhodogenum* Robak) isolated from wood pulp in Norway (Robak 1932). Over the next 30 years, four more species were described or renamed based on isolates from wood pulp, soil, basidiocarps, and air samples (Melin & Nannfeldt 1934, von Szilvinyi 1941, Malan 1949, Hughes 1958). Barron (1962) reviewed the genus, described four additional species, including *O. maius*, from peat soils in Ontario, Canada, and offered synonyms for several species, and provided a key for nine species. The number of species in the genus has grown to 23 and includes fungi isolated from soil, peat, decaying plant and fungal material, house dust, and air samples throughout the temperate regions of the world (Rice & Currah, in press). Most reports of *Oidiodendron* species are from temperate regions but there have been a few reports from the tropics (Ellis 1971, Hambleton *et al.* 1998, Calduch *et al.* 2004, Roose-Amsaleg *et al.* 2004).

Oidiodendron maius produces white colonies on a range of media. The colony colour is provided by the abundant arthroconidia that result from the fragmentation of branched hyaline hyphae formed at the apices of thick-walled, erect, melanized conidiophores that range from 30-500 µm tall (Figure 7.1A). Conidia are thin-walled, subglobose to elongate, cylindrical, or irregular, 2-5 x 1-2.5 µm, and have an asperulate perispore (Figure 7.1B) (Rice & Currah 2001, in press). They mature basipetally, i.e., with the youngest conidia at the base of the chains, closest to the conidiophore.

There are no reports of a sexual state associated with *O. maius* but morphological characters indicate a close affiliation to other taxa in the *Myxotrichaceae*: six teleomorph species within the *Myxotrichaceae* have *Oidiodendron* anamorphs (Hambleton *et al.* 1998, Rice & Currah, in press) and sterile ascomata with peridial elements resembling those formed by species of *Myxotrichum* Kunze can be induced when the species is grown on autoclaved lichen (Figure 7.1c) (Rice & Currah 2002). Furthermore, molecular evidence strongly suggests *O. maius* is affiliated with other species of *Myxotrichum* and *Oidiodendron* (Hambleton *et al.* 1998) and with the inoperculate discomycetes (*Leotiomycetes*) (e.g. Sugiyama *et al.* 1999, Mori *et al.* 2000, Gibas *et al.* 2002).

In this chapter, I first review the evidence suggesting that *O. maius* is a saprobe and then discuss its apparent role as an ericoid mycorrhizal fungus. Finally, I try to rationalize why isolation records of this Helotialean anamorph point towards its simultaneous occupation of mycorrhizal and saprobic roles and the significance of these roles.

7.3. *Oidiodendron maius* as a saprobe

From 1962 to 1989, *Oidiodendron maius* was known only from scattered records from soils and other decaying organic debris (Barron 1962, Nordgren *et al.* 1985) where it was presumed to occupy a saprobic niche, and from the ectomycorrhizal root tips of Sitka spruce (Schild *et al.* 1988). Although Schild *et al.* (1988) considered *O. maius* a cortical parasite of spruce, evidence of parasitism was not presented; instead, the evidence suggested that *O. maius* inhibited root pathogens, including *Phytophthora cinnamomi* Rands and *Heterobasidion annosum* (Fries) Brefeld. The inhibitory activity of *O. maius* towards root pathogens was accepted by Qian *et al.* (1998) who found that *O. maius* was a dominant inhabitant of the ectomycorrhizal root tips of Norway spruce under acidified conditions. The first report of *O. maius* from the roots of ericaceous shrubs was made in 1989 when it was isolated from ericoid mycorrhizal roots of *Rhododendron* (Douglas *et al.* 1989). Since then, most isolates of *O. maius* have been from presumably healthy ericaceous roots (e.g. Hambleton & Currah 1997, Currah *et al.* 1999, Monreal *et al.* 1999, Chambers *et al.* 2000, Usuki *et al.* 2003), but records of *O. maius* from other substrates continue to appear (e.g. Nilsson *et al.* 1992, Qian *et al.* 1998, Lumley *et al.* 2001, Thormann *et al.* 2001, 2004, Rice & Currah 2002).

Oidiodendron maius grows relatively rapidly on many artificial growth media with increases in colony radius of up to 1 mm/d on cornmeal agar (CMA) at pH 3 during periods of maximal growth (Rice & Currah 2001). It grows and sporulates readily on most media (Rice & Currah 2001, 2002) and can degrade a variety of carbon and nitrogen sources including tannic acid (a soluble phenolic compound), cellulose, starch (Rice & Currah 2001, in press, Thormann *et al.* 2002), chitin, pectin (Rice & Currah 2001, in press), and TWEEN 20 (a lipid-based detergent) (Rice & Currah, in press).

The presence of chitinases suggests *O. maius* may obtain nutrients (e.g. nitrogen) from polymeric glucosamines found in insects and fungi although there are no data to suggest parasitism of either group. *Oidiodendron maius* grows and sporulates luxuriantly on lichen (Rice & Currah 2002), on the context tissue of the basidiocarps of larger wood decay fungi [e.g. *Fomitopsis pinicola* (Swartz) Karsten], and on lipid-rich growth media and natural substrates. These observations suggest that *O. maius* is a saprobe on materials rich in lipids and chitin, such as the remains of fungi, lichens, and microfauna.

This suite of cultural characteristics is more indicative of a saprobic lifestyle rather than a mycorrhizal one that relies on biotrophically derived photosynthate (Hutchison 1990, 1991). Alternatively, because ecto- and ericoid mycorrhizal fungi have also been shown to degrade a variety of organic substrates (e.g. Bajwa & Read 1985, Northup *et al.* 1995, Bending & Read 1996, 1997, Aerts 2002, Leake *et al.* 2002, Olsson *et al.* 2002, Simard *et al.* 2002), these abilities may enable the absorption and transfer of organic or non-mineralized nutrients directly from the substrate to the cytoplasm of a host plant, effectively circumventing the mineralization steps in nutrient cycling (Northup *et al.* 1995, Aerts 2002, Leake *et al.* 2002). In this instance, it is the host that derives benefit and reciprocity for the fungus is not evident.

The ability to sporulate in pure culture is much less common for mycorrhizal fungi than saprobes, with all arbuscular and most ectomycorrhizal fungi unable to reproduce in the absence of their hosts (Read 2002). Endorhizal fungi allied to the *Helotiales* are notable exceptions (Addy *et al.* 2005). For example, *Rhizoscyphus ericae* (Read) Zhuang & Korf, an ericoid mycorrhizal fungus that also forms ectomycorrhizas (Vrålstad *et al.* 2000, 2002), produces chains of arthroconidia in culture, and in rare instances even forms apothecia (Hambleton *et al.* 1999). Unlike *O. maius*, *R. ericae* is unknown from non-mycorrhizal sources although this may be due to its variable cultural morphology, and the concomitant difficulties in making definitive identification of this fungus (Hambleton & Currah 1997, Hambleton & Sigler, in press).

The first record of *O. maius* was from "peat soil" (Barron 1962) and subsequent reports of this species from peat (e.g. Nilsson *et al.* 1992, Thormann *et al.* 2001, 2004, Rice & Currah 2002) remain more common than reports from other organic debris, such as wood (Lumley *et al.* 2001). *Oidiodendron maius* is more abundant in ectomycorrhizal root tips of spruce in blanket bogs than in mineral woodland soils (Schild *et al.* 1988) and in acidified rather than limed soils (Qian *et al.* 1998). The scant isolation data from other non-root materials is quite possibly the result of cultural biases. For example, when Rice & Currah (2002) compared the isolation frequency of this taxon using agar media and moist chambers, *O. maius* was the most abundant sporulating species appearing directly on *Sphagnum* peat but it was only rarely encountered when the same peat was placed on agar media. The addition of benomyl to the isolation media prevented the isolation of *O. maius* from ectomycorrhizal root tips (Schild *et al.* 1988) despite observations that *O. maius* is capable of growing on benomyl amended media (Rice & Currah 2002). Growth and sporulation of *O. maius* is restricted on rich artificial growth media, including potato dextrose and malt extract agars, that are commonly used to isolate fungi from substrates, further biasing against its recovery. Peat is a likely substrate on which to find *O. maius* because it is acidic and rich in many of the organic compounds, including tannic acid, cellulose, pectin, and chitin, that *O. maius* is able to degrade. The isolation history of *O. maius* coupled with *in vitro* studies of its behavior on *Sphagnum* peat suggest that *O. maius* is abundant in this material and may degrade large quantities of the substrate under natural conditions (Thormann 2001, Tsuneda *et al.* 2001, Piercey *et al.* 2002, Rice & Currah 2002, Thormann *et al.* 2002).

Two studies show that *O. maius* causes significant mass losses of *Sphagnum in vitro*, ranging from 2-3 % (Thormann 2001, Thormann *et al.* 2002) to 10-12 % (Piercey *et al.* 2002). Differences in mass loss between the studies may be explained by the use of intact *Sphagnum* by Thormann (Thormann 2001, Thormann *et al.* 2002) and homogenized *Sphagnum* by Piercey *et al.* (2002) or to strain-specific differences. Rice *et al.* (chapter 6, in prep) found that three isolates of *O. maius* varied dramatically in their abilities to cause mass loss of intact *Sphagnum* plants, with results ranging from negligible to almost 50 % but averaging about 15 %, suggesting that strain-specific differences may be significant. Piercey *et al.* (2002) compared mass losses caused by two isolates of *O. maius* (UAMH 8919, 8920) with those caused by other ericoid mycorrhizal fungi (*R. ericae* and an non-sporulating white to grey fungus designated "VWT") isolated from the roots of peatland and heathland *Ericaceae* and found that *O. maius* produced the greatest mass losses. Thormann *et al.* (2002) found that the mass losses caused by *O. maius* (UAMH 9749) were intermediate among five saprobic hyphomycetes [*O. maius*, "*Acremonium* cf. *curvulum*" [identified later as *Pochonia bulbillosa* (Gams & Malla) Zare & Gams, Thormann *et al.* 2004], *Penicillium thomii* Maire, *O. scytaloides* Gams & Söderström (= *O. chlamydosporicum* Morrall *sensu* Rice & Currah, in press), and *Trichoderma viride* Persoon] and greater than an unidentified basidiomycete. Tsuneda *et al.* (2001) used scanning electron microscopy to compare the ultrastructural patterns of decay of *Sphagnum* caused by *O. maius* and *P. bulbillosa*. The cell walls of *Sphagnum* are analogous to those in wood, consisting of cellulose microfibrils embedded in an amorphous matrix of phenolic polymers and polysaccharides (Tsuneda *et al.* 2001). Both species were capable of degrading *Sphagnum* leaves but displayed different decay patterns, with *O. maius* (UAMH 9749) eroding all cell wall components simultaneously (Figure 7.2) and *P. bulbillosa* degrading preferentially the amorphous matrix material (Tsuneda *et al.* 2001).

It is clear from the *in vitro* enzymatic studies, mass loss experiments, and scanning electron microscopy cited above that *O. maius* has the potential to degrade *Sphagnum* peat in nature. The abundance of *O. maius* conidia and conidiophores on peat (Rice & Currah 2002) and the relatively frequent isolation of *O. maius* from peat (Barron 1962, Thormann *et al.* 2001, 2004, Rice & Currah 2002) support the hypothesis that *O. maius* is an active component of the saprobic microfungal community in peatlands.

7.4. Ericoid Mycorrhizas

Cronquist (1988) recognized eight families within the globally distributed order *Ericales* that are integral components of many acidic, nutrient-poor ecosystems with organic soils. Four of these families, the *Ericaceae, Empetraceae, Monotropaceae*, and *Pyrolaceae*, are found in the northern hemisphere (Cronquist 1988). The four northern families and the *Epacridaceae*, a southern hemisphere taxon, are now included in a broadened concept of the *Ericaceae* based on molecular evidence (Kron 1996, Kron *et al.* 2002). Ericoid and ectendomycorrhizas are common within the *Ericaceae* but there are also reports of ectomycorrhizas (Largent *et al.* 1980, Smith *et al.* 1995, Horton *et al.* 1999) and arbuscular mycorrhizas (Koske *et al.* 1992).

Most *Ericaceae* are dwarf shrubs adapted to harsh ecosystems including bogs, heaths, alpine and arctic regions, and boreal forests (Hambleton 1998). These woody plants have leathery, perennial leaves that minimize nutrient loss. Ericoid mycorrhizal associations may enhance the success of many of these plants in nutrient-poor, acidic, phenol-rich, and heavy metal polluted soils (Perotto *et al.* 1995, Hambleton 1998, Hambleton & Currah 2000). The below-ground network consists of well developed mats of rhizomes and "hair roots" that form in the surface layers of organic soils (Read 1991). "Hair roots" have a narrow stele surrounded by an endodermis and one to two layers of cells, representing the cortex and/or epidermis, and lack root hairs (Read 1991, Smith & Read 1997). It is these external layers of cells that are colonized by ericoid mycorrhizal fungi (Perotto *et al.* 1995, Smith & Read 1997).

In ericoid mycorrhizal associations, fungi penetrate root cell walls and form an interface with cell membranes (Read 1991, Smith & Read 1997). Colonized cells become almost completely filled with hyphal complexes made up of densely intertwined, thin, lightly pigmented hyphae (Figure 7.3). Hyphae also extend out of the root and absorb nutrients, by decomposing organic matter within the soil, which are then supplied to the plant (Northup *et al.* 1995, Smith & Read 1997). The plant cell membranes fit closely around the hyphal complexes and nutrient and carbon exchange is believed to occur across these interfaces for about five weeks until both the plant cell cytoplasm and the fungal hyphae within the cell degenerate (Read 1991, Smith & Read 1997). Ericoid mycorrhizal fungi have also been shown to break down phenolic compounds and sequester heavy metal ions, detoxifying the soil for their plant partner (Read 1991, Perotto *et al.* 1995, Smith & Read 1997, Yang & Goulart 2000). While the benefits to the host plant are readily demonstrated in resynthesis studies, the benefits to the mycobiont (fungal partner) are more difficult to measure, but it is assumed that the mycobiont receives photosynthates from the host plant (Smith & Read 1997).

Identification of mycorrhizal fungal symbionts traditionally required recognition of the mycorrhizal structures formed, isolation of the fungi in culture, and resynthesis of the association (Smith & Read 1997, Hambleton 1998) but molecular methods have been used increasingly to identify mycorrhizal fungi (e.g. Gardes *et al.* 1991, Simon *et al.* 1992, Egger 1995, Clapp *et al.* 2002, Erland & Taylor 2002, Allen *et al.* 2003). Importantly, although these methods can enable identification of fungi that do not grow readily in culture, they cannot be used to confirm the functional nature of the relationship since many non-mycorrhizal fungi may be present in roots. The first fungi that were confirmed, through resynthesis experiments, to form ericoid mycorrhizal fungi were sterile and, thus, could not be identified with available techniques (Doak 1928, Bain 1937, Gordon 1937, McNabb 1961). In 1973, Pearson and Read reported that some of their ericoid mycorrhizal isolates produced zigzag chains of arthroconidia in culture and one of these produced small apothecia in pure cultures and in pot cultures with *Calluna vulgaris* (L.) Hull, an ericaceous shrub. This arthroconidial species was later named *Scytalidium vaccinii* Dalpé, Litten & Sigler (Dalpé *et al.* 1989) and the apothecial species was named *Pezizella ericae* Read (Read 1974). This species was later transferred to *Hymenoscyphus* Gray (Kernan & Finocchio 1983) and recently to *Rhizoscyphus* Zhuang & Korf, as *R. ericae* (Zhang & Zhuang 2004). *Scytalidium vaccinii* has been confirmed as the anamorph of *R. ericae* (Egger & Sigler 1993, Hambleton 1998, Hambleton *et al.* 1999). Hambleton and Currah (1997) described a series of isolates under "variable white taxon" (VWT) that were common endophytes in ericaceous roots. This taxon was later shown to have marked affinities to *R. ericae* but produced neither a teleomorph nor conidia in culture. Recently, three phylogenetically distinct species in the VWT complex have been recognized in a new anamorphic genus, "*Melinia*" (Hambleton & Sigler, in press). Allen *et al.* (2003) compared fungi detected in the roots of *Gaultheria shallon* Pursh using culturing and molecular (DNA) methods and found that even though most of the cloned fungi represented an unknown species of *Sebacina* Tulasne & Tulasne, this fungus did not appear in any of the cultures. Fungi that were culturable included *R. ericae* and an isolate tentatively identified as a species of *Capronia* Saccardo (Allen *et al.* 2003). As our detection techniques improve, it is likely that more taxa will be described as ericoid mycorrhizal endophytes.

Species of *Oidiodendron* are also reported from ericoid mycorrhizas (Pearson & Read 1973, Couture *et al.* 1983, Dalpé 1986, 1989, 1991, Douglas *et al.* 1989, Stoyke & Currah 2001, Xiao & Berch 1992, Currah *et al.* 1993, Johansson 1994, 2001, Perotto *et al.* 1995, 1996, Hambleton & Currah 1997, Currah *et al.* 1999, Monreal *et al.* 1999, Chambers *et al.* 2000, Usuki *et al.* 2003). While many of the early reports implicated *O. griseum* Robak in the associations, later DNA analyses indicated that most, if not all, of these reports were misidentified strains of *O. maius* (Hambleton & Currah 1997, Hambleton *et al.* 1998).

Mycorrhizal resyntheses between host plant and fungi isolated from their ericoid mycorrhizas are generally assumed to be the definitive indicator that a fungus is mycorrhizal but assumptions based on these data are tenuous at best. The *Ericaceae* is particularly problematic in this regard because, in axenic situations at least, the family appears able to permit a wide range of fungi into the peripheral cells of hair roots where they form the typical coiled "infection units" that characterize ericoid mycorrhizas. For example, Dalpé (1986, 1989, 1991) found that ericoid mycorrhizas formed with blueberries (*Vaccinium angustifolium* Ait.) and *Myxotrichum setosum* (Eidam) Orr & Plunkett, *Oidiodendron cerealis* (Thümen) Barron, *O. chlamydosporicum, O. citrinum* Barron, *O. flavum* von Szilvinyi, *O. griseum, O. periconioides* Morrall, *O. rhodogenum, O. scytaloides, Pseudogymnoascus roseus* Raillo (all members of the *Myxotrichaceae, Leotiomycetes*), and the unrelated species *Gymnascella dankaliensis* (Castellani) Currah (a member of the *Gymnoascaceae, Eurotiomycetes*). Salal (*Gaultheria shallon*) has been shown to form *in vitro* mycorrhizal associations with *Acremonium strictum* Gams where *A. strictum* supplied organic nitrogen and enhanced the growth of the host plants (Xiao & Berch 1999). Ericaceous plants may "prefer" some fungi over others in the field but when constrained, as in a culture situation, can form mycorrhizal relationships with or exploit a range of different fungal species.

7.5. *Oidiodendron maius* as an ericoid mycorrhizal fungus

Oidiodendron maius has been isolated from ericaceous plants from heathlands, peatlands, and forests in North America, Europe, Japan, and Australia (e.g. Perotto *et al.* 1996, Hambleton & Currah 1997, Hambleton *et al.* 1998, Currah *et al.* 1999, Chambers *et al.* 2000, Usuki *et al.* 2003). While the widespread isolation of *O. maius* from the roots of apparently healthy ericaceous plants supports the hypothesis that it may be mycorrhizal and, as such, either a mutualist or a commensalist, it does not confirm the nature of the association. Resynthesis studies have been done to attempt to assess the morphological and functional aspects of the relationship (Douglas *et al.* 1989, Xiao & Berch 1995, 1999, Yang *et al.* 1998, Monreal *et al.* 1999, Bergero *et al.* 2000, Yang & Goulart 2000, Johansson 2001, Starrett *et al.* 2001, Piercey *et al.* 2002, Yang *et al.* 2002) and using other *Oidiodendron* species (Couture *et al.* 1983, Dalpé 1986, 1989, 1991, Currah *et al.* 1993, Xiao & Berch 1995, Monreal *et al.* 1999, Starrett *et al.* 2001). These have used a range of ericaceous shrubs and the results have included positive, negative, and neutral effects on host plant growth. Many studies have not explored the functional nature of the relationship but have noted that hyphal complexes, morphologically characteristic of ericoid mycorrhizas, have been observed in roots of various ericaceous shrubs colonized by *Oidiodendron* species (Dalpé 1986, 1989, 1991, Douglas *et al.* 1989, Currah *et al.* 1993, Xiao & Berch 1995, Johansson 2001, Hambleton, pers. comm.), including *Vaccinium vitis-idaea* L. (Figure 7.3). While the plants in these studies appeared healthy, the functional nature of the relationship between the fungi and the hosts is not known.

Physiological evidence to support the mycorrhizal nature of the association between *O. maius* and ericaceous shrubs has been obtained from resynthesis studies. Yang *et al.* (1998) found that *O. maius* (UAMH 9263) did not affect the growth of blueberries, but later studies using the same isolate of *O. maius* and the same plant found positive effects on plant growth (Yang & Goulart 2000, Yang *et al.* 2002), indicating that the nature of the relationship between *O. maius* and ericaceous shrubs may vary within fungal isolates. Inoculation of salal (*Gaultheria shallon*) with four isolates of *O. maius* increased plant biomass regardless of the nitrogen source supplied (Xiao & Berch 1999). Inoculation with *O. maius* increased blueberry root and shoot dry mass as well as plant access to organic nitrogen (Yang *et al.* 2002) and has also been shown to reduce aluminum uptake and increase the cation exchange capacity of blueberries (Yang & Goulart 2000).

Despite the results cited above, the evidence suggesting a mycorrhizal role for *O. maius* is equivocal. Several resynthesis studies (Dalpé 1991, Bergero *et al.* 2000, Piercey *et al.* 2002) have not yielded the distinctive infection units that characterize the ericoid mycorrhizal association. These observations may be explained by the strong saprobic abilities of *O. maius* compared with other ericoid mycorrhizal fungi (Piercey *et al.* 2002), by strain-specific effects, or by the nutrient sources supplied. *Oidiodendron maius* is likely to acquire sufficient carbon from the substrate (for example, *Sphagnum* peat in the study by Piercey *et al.* 2002) and may not rely on the host for nutrition in these axenic cultures. Other resynthesis studies have shown either neutral (Yang *et al.* 1998) or negative effects (Starrett *et al.* 2001) on the plants. Starrett *et al.* (2001) inoculated microshoots of mountain andromeda [*Pieris floribunda* (Pursh) Benth. & Hook.] with the "ericoid mycorrhizal fungi" *R. ericae*, *O. maius* (ATCC 66504), *O. griseum*, and an unidentified *Oidiodendron* species, and found that inoculation with all of these species caused shoot necrosis, but that this effect could be reduced by providing the fungi with an alternative carbon source. Mitigation of shoot necrosis varied with the carbon source and fungal isolate. Adding sucrose to the medium prevented *R. ericae*, but not the *Oidiodendron* species, from causing shoot necrosis while adding a peat-vermiculite mixture reduced the shoot necrosis caused by the *Oidiodendron* species. Additionally, the *Oidiodendron* species did not induce root formation by the microshoots to the same extent as *R. ericae*, leading Starrett *et al.* (2001) to conclude that the *Oidiodendron* species were pathogenic rather than mycorrhizal.

Notably, none of the preceding studies have investigated possible benefits to the mycobiont, so the mutualistic nature of the association has not been demonstrated conclusively. It is possible that the relationship is physiologically similar to the dynamics in orchid mycorrhizas in which the orchid "exploits" its saprobic, ectomycorrhizal, or plant pathogenic mycobiont (e.g. Rasmussen 1995, McKendrick *et al.* 2000) or to the epiparasitic relationship of monotropes (non-photosynthetic *Ericaceae*) to ectomycorrhizal trees via shared ectomycorrhizal fungi (Bidartondo *et al.* 2000). Many *Ericaceae*, similar to the *Orchidaceae* and the monotropes, are microspermous (e.g. *Rhododendron, Menziesia*). Perhaps the adoption of microspermy is a consequence of the host plants' ability to exploit fungi as a source of nutrients and, thus, ericoid mycorrhizal associations may be a part of a mycoheterotrophic evolutionary trajectory. The discovery of *Sebacina*, a basidiomycete genus known to form orchid mycorrhizas, in ericoid mycorrhizal roots of salal (Allen *et al.* 2003) is another indication of the similarities between ericoid and orchid mycorrhizal systems (Currah *et al.* 1990, McKendrick *et al.* 2002). Alternatively, the interaction may be variable, sometimes benefiting either one of the partners and at other times benefiting both.

The nature of the relationship between *O. maius* and members of the *Ericaceae* is clearly complex and context dependent. Future research involving physiological assessment in laboratory, greenhouse, and field conditions coupled with morphological and molecular assessments in roots (Hambleton & Currah 2000) is required to identify and quantify possible benefits to both partners and to elucidate the factors determining the functional aspects of the relationship. For example, the transfer of radiolabeled carbon and nutrients between the partners could be traced under various conditions to determine whether *O. maius* ever obtains photosynthate or if the plant receives any fungal-derived carbon. Additionally, *in vitro* studies could determine other potential benefits to either partner, such as competitive and growth advantages for *O. maius* and pathogen resistance for the plant. The potential role of ericoid mycorrhizal fungi in symbiotic seed germination should be examined.

7.6. Significance and Relevance

The occupation of multiple niches within the same environment would confer survival and competitive advantages on *O. maius* by providing a series of refuges; however, this hypothesis has not been tested experimentally. During periods of host plant dormancy, *O. maius* should be able to thrive as a saprobe while host plant roots may serve as a refuge from competition from other saprobes and as a source of inoculum for senescing surface peat where ericaceous roots are abundant. The prevalence of *O. maius* as a saprobe within the peat likely ensures rapid colonization of new ericaceous roots, perhaps at the expense of other species that are less adapted to degrading the surrounding substrate.

Ericoid and ectomycorrhizal fungi can degrade a variety of complex organic substrates (Bajwa & Read 1985, Read 1991, Northup *et al.* 1995, Bending & Read 1996, 1997, Smith & Read 1997, Aerts 2002, Leake *et al.* 2002, Olsson *et al.* 2002, Simard *et al.* 2002), with the abilities of ericoid mycorrhizal fungi possibly exceeding those of ectomycorrhizal fungi (Bajwa & Read 1985, Bending & Read 1996, 1997, Smith & Read 1997). These abilities are predicted to aid in host plant nutrition by allowing the plant direct access to organic nutrient sources (Bajwa & Read 1985, Xiao & Berch 1999, Yang *et al.* 2002). Inorganic sources of nitrogen are scarce and organic sources relatively abundant when decomposition is slow, as in peatlands and heathlands, and when leaching is common (Perotto *et al.* 1995). Ericoid mycorrhizal fungi often produce phosphatases, enabling them to access organic phosphorus and transfer it to their hosts (Aerts 2002). Organic molecules also include carbon and the ericaceous shrubs in these environments may rely on their endophytes to supply them with sufficient carbon and nutrients obtained from the organic sources (Northup *et al.* 1995, Xiao & Berch 1999, Yang *et al.* 2002). This carbon could help sustain the plants during periods of low photosynthesis. The abilities of ericoid mycorrhizal fungi, including *O. maius*, to access carbon and nutrients from organic debris could reduce their reliance on host plant photosynthates for carbon (Piercey *et al.* 2002) while still supplying the host plant with nutrients.

The transfer of nutrients from organic matter to ericaceous shrubs via ericoid mycorrhizal fungi, such as *O. maius*, has important implications for nutrient cycling in ecosystems, such as peatlands, where decomposition is slow and carbon and nutrients are sequestered in organic debris (Northup *et al.* 1995). *Sphagnum* decomposes slowly with relatively few fungi having the ability to cause significant mass losses (Thormann 2001, Tsuneda *et al.* 2001, Thormann *et al.* 2002). Decomposition of *Sphagnum* by *O. maius* may release a significant amount of carbon and nutrients from the peat. Instead of releasing carbon into the atmosphere and making the nitrogen and phosphorus available for general plant uptake, this carbon, nitrogen, and phosphorus can be supplied directly to the ericaceous shrubs, giving them a competitive advantage over their neighbouring plants (Aerts 2002, Leake *et al.* 2002).

Other *Oidiodendron* species are able to form ericoid mycorrhizal associations *in vitro* (Dalpé 1986, 1989, 1991, Currah *et al.* 1993). Species of *Oidiodendron* are the asexual states of myxotrichoid ascomycetes, and some of these (e.g. *Myxotrichum setosum, Pseudogymnoascus* *roseus*) and other anamorphs, including species of *Geomyces*, also produce *in vitro* ericoid mycorrhizal associations (Dalpé 1989). However, only two or perhaps three species of *Oidiodendron* have been reported from ericaceous roots *in situ*. *Oidiodendron griseum* was reported from ericaceous roots (Couture *et al.* 1983, Stoyke & Currah 1991, Xiao & Berch 1992, Johansson 1994) but most of these isolates have been reidentified as *O. maius* (Hambleton & Currah 1997, Hambleton *et al.* 1998). Currah *et al.* (1993) isolated *O. periconioides* from the roots of *Rhododendron brachycarpum* Don. grown in pot cultures containing peat. The remaining species are known only as saprobes but since they share morphological characters, including dendritic arthroconidia and cage-like cleistothecial ascomata, and ecological characters, including the ability to degrade a variety of plant- and animal-based polymers and a predilection for cool, acidic conditions (Rice & Currah, in press), it is possible that these taxa could play biologically similar and significant roles to *O. maius* in cool, acidic, organic soils and peat. Additional surveys of ericoid mycorrhizal endophytes should employ a broad range of isolation and detection protocols to maximize the recovery of a wide variety of fungi.

The occupation of multiple niches by *O. maius* appears to parallel the situation observed for *Phialocephala fortinii* Wang & Wilcox. Usually considered a dark septate endophyte, *P. fortinii* is isolated most frequently from healthy roots of woody plants (e.g. Stoyke & Currah 2001, Menkis *et al.* 2004, Piercey *et al.* 2004, Addy *et al.* 2005) and, until recently, was unknown as a saprobe. However, Menkis *et al*. (2004) have isolated *P. fortinii* from healthy wood in pine stems, suggesting a possible role as a systemic endophyte, and in birch snags and birch and pine stumps where it is presumably occupying a saprobic niche (Menkis *et al*. 2004), perhaps as an agent of soft rot (Sieber 2002, Menkis *et al*. 2002).

7.7. Conclusions

Oidiodendron maius forms associations with ericaceous shrubs but the nature of the relationship remains uncertain. Is it a mutualistic mycorrhizal association or a case of parasitism of the fungus by the plant? *In vitro* studies indicate that *O. maius* can improve host plant growth both by aiding plant nutrition and detoxifying the soil environment but the benefits to *O. maius* are unclear and future research is necessary to investigate the benefits to both partners and demonstrate what environmental conditions determine the functional nature of the relationship. *Oidiodendron maius* has the potential to degrade complex organic polymers within the soil; thus, it seems unlikely that it would rely on host photosynthate for survival. However, it is possible that *O. maius* receives some photosynthate, which may supplement saprobically-derived carbon, potentially giving *O. maius* a competitive or growth advantage over other soil fungi. The tendency towards microspermy in the *Ericaceae* and the saprobic abilities of ericoid mycorrhizal endophytes suggests that the ericoid mycorrhizal association may represent another example of controlled parasitism of a fungal partner by the host plant. Entrapment of *O. maius* may confer a competitive advantage on the host plants by increasing the supply or organically-derived nutrients, which might be limiting to other plants, and by supplementing host plant photosynthesis with fungal-derived carbon. The ability to occupy multiple niches may be best illustrated by the situation in peatlands, where *O. maius* acts as a saprobe on the *Sphagnum* peat matrix that surrounds the roots of the ericaceous shrubs in which it is likely a mycorrhizal endophyte. This flexibility likely confers competitive and survival advantages on both *O. maius* and its hosts. Other saprobic species, including those in *Oidiodendron* and *Geomyces* along with their myxotrichaceous sexual states, that have the ability to form ericoid mycorrhizal associations *in vitro*, and other endophytic fungi, including *P. fortinii* and *R. ericae*, isolated primarily from roots, may also occupy multiple niches in some environments.

Figure 7.1. Morphology of *Oidiodendron maius* in axenic culture.

A. Tall, erect, melanized conidiophores and small, hyaline arthroconidia of UAMH 9749 viewed under light microscopy. Bar = 40 µm. **B**. Chains of arthroconidia of UAMH 8920 showing asperulate ornamentation visible under scanning electron microscopy. Bar = 5 µm. **C**. Sterile peridial elements produced by UAMH 9749 crossed with UAMH 10460 on sterilized thalli of *Cladonia mitis*. The cage-like peridial elements resemble the cleistothecia of species of *Myxotrichum*. Bar = 80 µm.

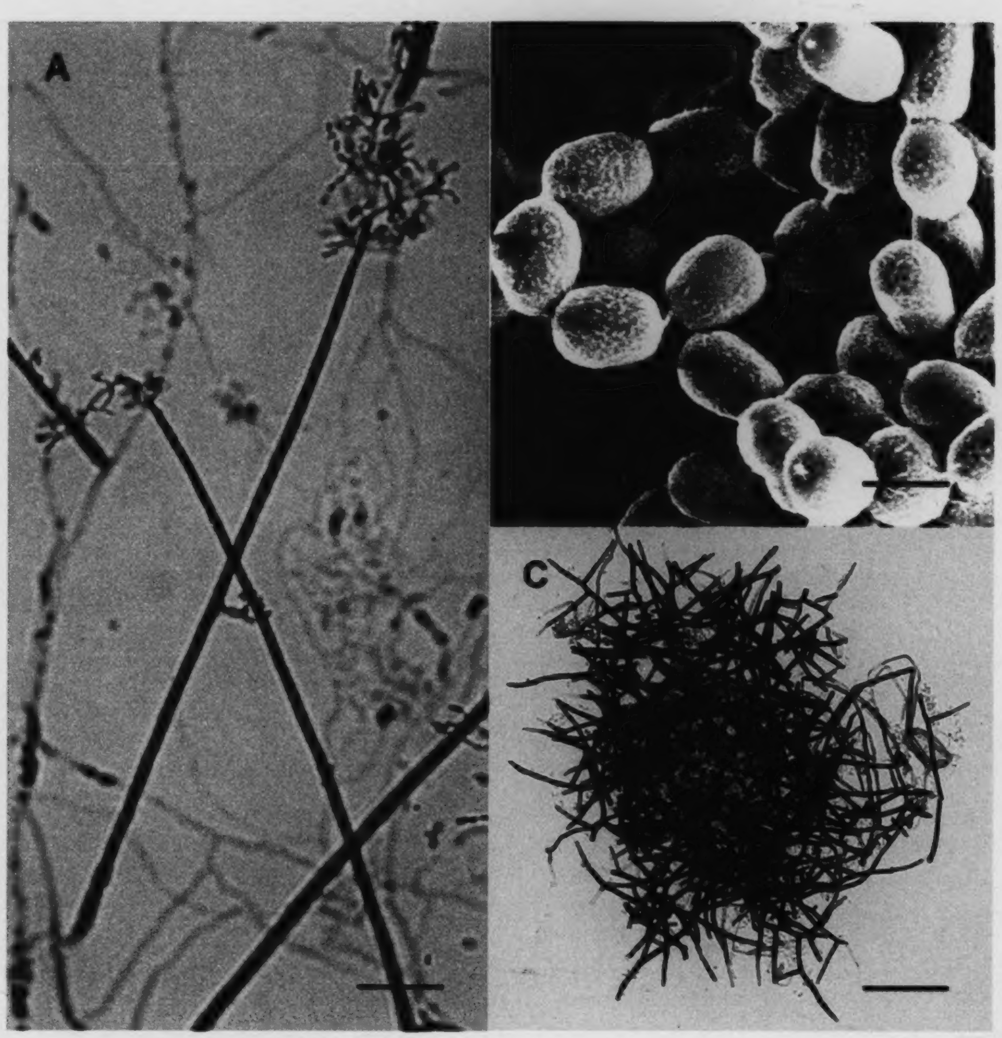

A
C

Figure 7.2. Degradation of *Sphagnum fuscum* leaf cell walls by *Oidiodendron maius* (UAMH 9749). Reproduced with permission from Tsuneda *et al.* 2001.

A. Affected cell wall showing finely wavy deformations (arrows). Bar = 3 µm. **B**. Severely distorted leaf cell wall (arrow). Note autolyzing hypha (arrowhead) and degraded leaf cell wall in the immediate vicinity. H = hypha, C = conidia. **C**. Localized voids (arrows) and hyphae (H) emerged through the leaf cell wall. Bar = 5 µm. **D**. More or less simultaneous degradation of the leaf cell wall by a hypha (H). Arrows indicate localized voids. **E**. Enlarged view of an area showing the simultaneous degradation (arrow). Arrowheads point to autolyzing hyphae. H = sound, turgid hyphae. Bar = 2 µm.

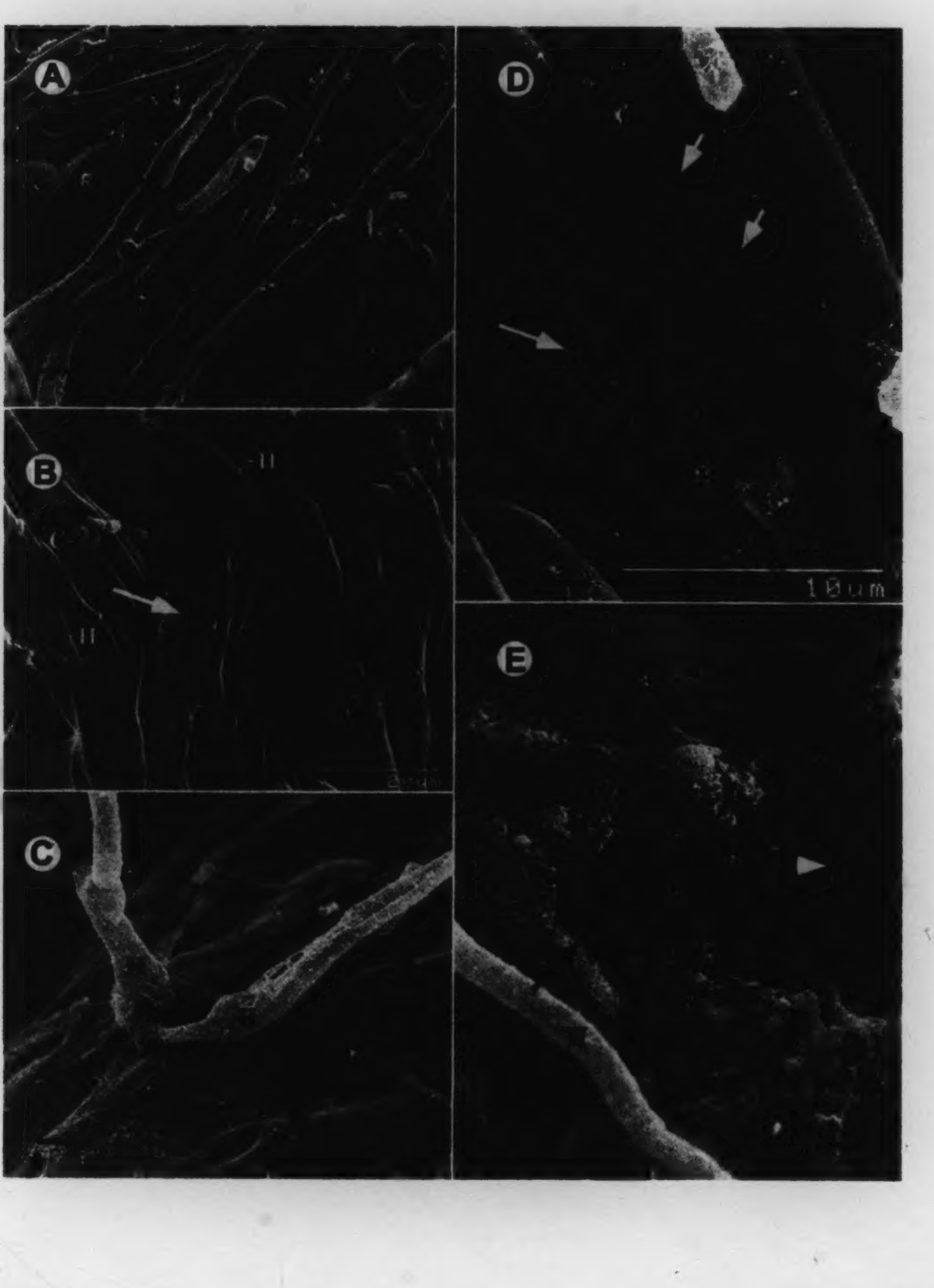
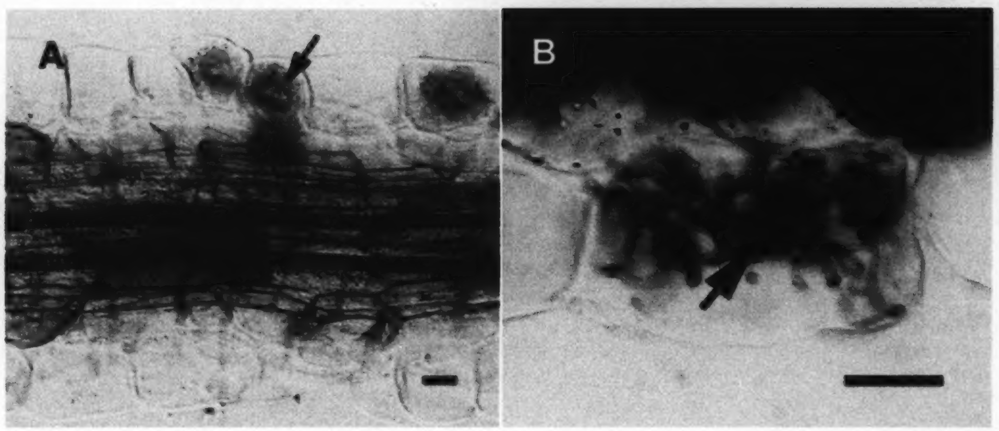

A
B
II
II
C
D
10um
E

Figure 7.3. Light micrographs of *Oidiodendron maius* (Hambleton personal collection, S-272a) colonizing the roots of *Vaccinium vitis-idaea* in a resynthesis study (Hambleton, unpublished). Images provided by Sarah Hambleton.

A. Longitudinal section of a mycorrhizal root showing hyphal complexes (arrow) formed in the outer layer of root cells. Bar = 10 µm. **B**. Close up of hyphal complex (arrow) formed in the root cell. Bar = 10 µm.


A
B

7.8. Literature Cited

Addy HD, Piercey MM, Currah RS (2005). Microfungal endophytes in roots. *Canadian Journal of Botany* **83**: 1–13.

Aerts R (2002). The role of various types of mycorrhizal fungi in nutrient cycling and plant competition. In: van der Heijden MGA, Sanders IR (eds) *Ecological Studies, vol 157. Mycorrhizal Ecology*. Springer-Verlag, Berlin. pp. 117–133.

Allen TR, Millar T, Berch SM, Berbee ML (2003). Culturing and direct DNA extraction find different fungi from the same ericoid mycorrhizal roots. *New Phytologist* **160**: 255–272.

Bain HF (1937). Production of synthetic mycorrhiza in the cultivated cranberry. *Journal of Agricultural Research* **55**: 811–835.

Bajwa R, Read DJ (1985). The biology of mycorrhiza in the *Ericaceae*. IX. Peptides as nitrogen sources for the ericoid endophyte and for mycorrhizal and non-mycorrhizal plants. *New Phytologist* **101**: 459–467.

Barron GL (1962). New species and new records of *Oidiodendron*. *Canadian Journal of Botany* **40**: 589–607.

Bending GD, Read DJ (1996). Nitrogen mobilization from tannin-protein complexes by ericoid and ectomycorrhizal fungi. *Soil Biology and Biochemistry* **28**: 1603–1612.

Bending GD, Read DJ (1997). Lignin and soluble phenolic degradation by ectomycorrhizal and ericoid mycorrhizal fungi. *Mycological Research* **101**: 1348–1354.

Bergero R, Perotto S, Girlanda MM, Vidano G, Luppi AM (2000). Ericoid mycorrhizal fungi are common root associates of a Mediterranean ectomycorrhizal plant (*Quercus ilex*). *Molecular Ecology* **9**: 1639–1649.

Bidartondo MI, Kretzer AM, Pine EM, Bruns TD (2000). High root concentrations and uneven ectomycorrhizal diversity near *Sarcodes sanguinea* (*Ericaceae*): A cheater that stimulates its victims? *American Journal of Botany* **87**: 1783–1788.

Calduch M, Gené J, Cano J, Stchigel A, Guarro J (2004). Three new species of *Oidiodendron* Robak from Spain. *Studies in Mycology* **50**: 159–170.

Chambers SM, Liu G, Cairney WG (2000). ITS rDNA sequence comparison of ericoid mycorrhizal endophytes from *Woollsia pungens*. *Mycological Research* **104**: 168–174.

Clapp JP, Helgason T, Daniell TJ, Young JPW (2002). Genetic studies of the structure and diversity of arbuscular mycorrhizal fungal communities. In: van der Heijden MGA, Sanders IR (eds) *Ecological Studies, vol 157. Mycorrhizal Ecology*. Springer-Verlag, Berlin. pp. 201–224.

Couture M, Fortin JA, Dalpé Y (1983). *Oidiodendron griseum* Robak: an endophyte of ericoid mycorrhiza in *Vaccinium* spp. *New Phytologist* **95**: 375–380.

Cronquist A (1988). *The Evolution and Classification of Flowering Plants*. 2nd Edition. New York Botanic Garden, New York, USA.

Currah RS (1985). Taxonomy of the *Onygenales*: *Arthrodermataceae, Gymnoascaceae, Myxotrichaceae* and *Onygenaceae*. *Mycotaxon* **24**: 1–216.

Currah RS, Niemi M, Huhtinen S (1999). *Oidiodendron maius* and *Scytalidium vaccinii* from the mycorrhizas of *Ericaceae* in northern Finland. *Karstenia* **39**: 65–68.

Currah RS, Smreciu ES, Hambleton S (1990). Mycorrhizae and mycorrhizal fungi of boreal species of *Planthera* and *Coeloglossum* (*Orchidaceae*). *Canadian Journal of Botany* **68**: 1171–1181.

Currah RS, Tsuneda A, Murakami S (1993). Conidiogenesis in *Oidiodendron periconioides* and ultrastructure of ericoid mycorrhizas formed with *Rhododendron brachycarpum*. *Canadian Journal of Botany* **71**: 1481–1485.

Dalpé Y (1986). Axenic synthesis of ericoid mycorrhiza in *Vaccinium angustifolium* Ait. by *Oidiodendron* species. *New Phytologist* **103**: 391–396.

Dalpé Y (1989). Ericoid mycorrhizal fungi in the *Myxotrichaceae* and *Gymnoascaceae*. *New Phytologist* **113**: 523–527.

Dalpé Y (1991). Statut endomycorrhizien du genre *Oidiodendron*. *Canadian Journal of Botany* **69**: 1712–1714.

Dalpé Y, Litten W, Sigler L (1989). *Scytalidium vaccinii* sp. nov., an ericoid endophyte of *Vaccinium angustifolium* roots. *Mycotaxon* **35**: 371–377.

Doak KD (1928). The mycorrhizal fungi of *Vaccinium*. *Phytopathology* **18**: 148.

Douglas AE, Smith DC (1989). Are endosymbioses mutualistic? *Trends in Ecology and Evolution* **4**: 350–352.

Douglas GC, Heslin MC, Reid C (1989). Isolation of *Oidiodendron maius* from *Rhododendron* and ultrastructural characteristics of synthesized mycorrhizas. *Canadian Journal of Botany* **67**: 2206–2212.

Egger KN (1995). Molecular analysis of ecto-mycorrhizal fungal communities. *Canadian Journal of Botany* **73**: S1415–S1422.

Egger KN, Sigler L (1993). Relatedness of the ericoid endophytes *Scytalidium vaccinii* and *Hymenoscyphus ericae* inferred from analysis of ribosomal DNA. *Mycologia* **85**: 219–230.

Ellis MB (1971). *Dematiaceous Hyphomycetes*. Commonwealth Agricultural Bureaux, United Kingdom.

Erland S, Taylor AFS (2002). Diversity of ecto-mycorrhizal fungal communities in relation to the abiotic environment. In: van der Heijden MGA, Sanders IR (eds) *Ecological Studies, vol 157. Mycorrhizal Ecology*. Springer-Verlag, Berlin. pp. 163–200.

Gardes M, White TJ, Fortin JA, Bruns TD, Taylor JW (1991). Identification of indigenous and introduced symbiotic fungi in ecto-mycorrhizas by amplification of nuclear and mitochondrial ribosomal DNA. *Canadian Journal of Botany* **69**: 180–190.

Gibas CFC, Sigler L, Summerbell RC, Currah RS (2002). Phylogeny of the genus *Arachnomyces* and its anamorphs and the establishment of *Arachnomycetales*, a new eurotiomycete order in the *Ascomycota*. *Studies in Mycology* **47**: 131–139.

Gordon HD (1937). Mycorrhiza in *Rhododendron*. *Annals of Botany* **1**: 593–613.

Hambleton S (1998). *Mycorrhizas of the Ericaceae: Diversity and Systematics of the Mycobionts*. PhD Dissertation, University of Alberta, Edmonton, AB, Canada.

Hambleton S, Currah RS (1997). Fungal endophytes from the roots of alpine and boreal *Ericaceae*. *Canadian Journal of Botany* **75**: 1570–1581.

Hambleton S, Currah RS (2000). Molecular characterization of the mycorrhizas of woody plants. In: Jain SM, Minocha SC (eds) *Molecular Biology of Woody Plants*, vol 2. Kluwer Academic Publishers, Netherlands. pp. 351–373.

Hambleton S, Egger KN, Currah RS (1998). The genus *Oidiodendron*: species delimitation and phylogenetic relationships based on nuclear ribosomal DNA analysis. *Mycologia* **90**: 854–869.

Hambleton S, Huhtinen S, Currah RS (1999). *Hymenoscyphus ericae*: a new record from western Canada. *Mycological Research* **103**: 1391–1397.

Hambleton S, Sigler L (in press). *Melinia*, a new anamorph genus for root-associated fungi with phylogenetic affinities to *Rhizoscyphus ericae* (≡*Hymenoscyphus ericae*), *Leotiomycetes*. *Studies in Mycology*. (accepted 2004).

Hoosbeek M, van Breeman N, Berendse F, Grosvernier P, Vasander H, Wallén B (2001). Limited effect of increased atmospheric CO_2 concentration on ombrotrophic bog vegetation. *New Phytologist* **150**: 459–463.

Horton TR, Bruns TD, Parker VT (1999). Ectomycorrhizal fungi associated with *Arctostaphylos* contribute to *Pseudotsuga menziesii* establishment. *Canadian Journal of Botany* **77**: 93–102.

Hughes SJ (1958). Revisiones hyphomycetum aliquot cum appendice de nominibus rejiciendis. *Canadian Journal of Botany* **36**: 727–836.

Hutchison LJ (1990). Studies on the systematics of ectomycorrhizal fungi in axenic culture. II. The enzymatic degradation of selected carbon and nitrogen compounds. *Canadian Journal of Botany* **68**: 1522–1530.

Hutchison LJ (1991). Description and identification of cultures of ectomycorrhizal fungi found in North America. *Mycotaxon* **42**: 387–504.

Johansson M (1994). Quantification of mycorrhizal infection units in roots of *Calluna vulgaris* (L.) Hull from Danish heathlands. *Soil Biology and Biochemistry* **26**: 557–566.

Johansson M (2001). Fungal associations of Danish *Calluna vulgaris* roots with special reference to ericoid mycorrhiza. *Plant and Soil* **231**: 225–232.

Kernan MJ, Finocchio AF (1983). A new discomycete associated with the roots of *Monotropa uniflora* (*Ericaceae*). *Mycologia* **75**: 916–920.

Koske RE, Gemma JN, Englander L (1990). Vesicular-arbuscular mycorrhizae in Hawaiian Ericales. *American Journal of Botany* **77**: 64–68.

Kron KA (1996). Phylogenetic relationships of the *Empetraceae, Epacridaceae, Ericaceae, Monotropaceae*, and *Pyrolaceae*: evidence from nuclear ribosomal 18S sequence data. *Annals of Botany* **77**: 293–303.

Kron KA, Judd WS, Stevens PF, Crayne DM, Anderberg AA, Gadek PA, Quinn CJ, Luteyn JL (2002). Phylogenetic classification of *Ericaceae*: molecular and morphological evidence. *Botanical Review* **68**: 335–423.

Largent DL, Sugihara N, Wishner C (1980). Occurrence of mycorrhizae on ericaceous and pyrolaceous plants in northern California. *Canadian Journal of Botany* **58**: 2274–2279.

Leake JR, Donnelly DP, Boddy L (2002). Interactions between ecto-mycorrhizal and saprotrophic fungi. In: van der Heijden MGA, Sanders IR (eds) *Ecological Studies, vol 157. Mycorrhizal Ecology*. Springer-Verlag, Berlin. pp. 345–372.

Lumley TC, Gignac LD, Currah RS (2001). Microfungus communities of white spruce and trembling aspen logs at different stages of decay in disturbed and undisturbed sites in the boreal mixedwood region of Alberta. *Canadian Journal of Botany* **79**: 76–92.

Malan CE (1949). Su un nuovo reperto di *Dicyma ambigua* Peyronel e sulla posizione sistematica di questa specie. *Giornale Botanico Italiano* **56**: 735–738.

McKendrick SL, Leake JR, Read DJ (2000). Symbiotic germination and development of mycoheterotrophic plants in nature: transfer of carbon from ectomycorrhizal *Salix repens* and

Betula pendula to the orchid *Corallorhiza trifida* through shared hyphal connections. *New Phytologist* **145**: 539–548.

McKendrick SL, Leake JR, Taylor DL, Read DJ (2002). Symbiotic germination and development of the myco-heterotrophic orchid *Neottia nidus-avis* in nature and its requirement for locally distributed *Sebacina*. *New Phytologist* **154**: 233–247.

McNabb RFR (1961). Mycorrhiza in the New Zealand *Ericales*. *Australian Journal of Botany* **9**: 57–61.

Melin E, Nannfeldt JA (1934). Researches into the bluing of ground woodpulp. *Saertryck ur Svenska Skogsvårdsföreningens Tidskrift Hafte* **3-4**: 397–616.

Menkis A, Allmer J, Vasiliauskas R, Lygis V, Stenlid J, Finlay R (2004). Ecology and molecular characterization of dark septate fungi in roots, living stems, coarse and fine woody debris. *Mycological Research* **108**: 965–973.

Monreal M, Berch SM, Berbee M (1999). Molecular diversity of ericoid mycorrhizal fungi. *Canadian Journal of Botany* **77**: 1580–1594.

Mori Y, Sato Y, Takamatsu S (2000). Molecular phylogeny and radiation time of *Erysiphales* inferred from the nuclear ribosomal DNA sequences. *Mycoscience* **41**: 437–447.

Nilsson M, Bååth E, Söderström B (1992). The microfungal communities of a mixed mire in northern Sweden. *Canadian Journal of Botany* **70**: 272–276.

Nordgren A, Bååth E, Söderström B (1985). Soil microfungi in an area polluted by heavy metals. *Canadian Journal of Botany* **63**: 448–455.

Northup RR, Zengshou Y, Dahlgren RA, Vogt KA (1995). Polyphenol control of nitrogen release from pine litter. *Nature* **377**: 227–229.

Olsson PA, Jakobsen I, Wallander H (2002). Foraging and resource allocation strategies of mycorrhizal fungi in a patchy environment. In: van der Heijden MGA, Sanders IR (eds) *Ecological Studies, vol 157. Mycorrhizal Ecology*. Springer-Verlag, Berlin. pp. 93–115.

Pearson V, Read DJ (1973). The biology of mycorrhiza in *Ericaceae*. I. The isolation of the endophyte and synthesis of mycorrhizas in aseptic culture. *New Phytologist* **72**: 371–379.

Perotto S, Actis-Perino E, Perugini J, Bonfante P (1996). Molecular diversity of fungi from ericoid mycorrhizal roots. *Molecular Ecology* **5**: 123–131.

Perotto S, Perotto R, Faccio A, Schubert A, Varma A, Bonfante P (1995). Ericoid mycorrhizal fungi: cellular and molecular bases of their interactions with the host plant. *Canadian Journal of Botany* **73**: S557–S568.

Peteet D, Andreev A, Bardeen W, Mistretta F (1998). Long-term arctic peatland dynamics, vegetation and climate history of the Pur-Taz region, Western Siberia. *Boreas* **27**: 115–126.

Piercey MM, Graham SW, Currah RS (2004). Patterns of genetic variation in *Phialocephala fortinii* across a broad latitudinal transect in Canada. *Mycological Research* **108**: 955–964.

Piercey MM, Thormann MN, Currah RS (2002). Saprobic characteristics of three fungal taxa from ericalean roots and their association with the roots of *Rhododendron groenlandicum* and *Picea mariana* in culture. *Mycorrhiza* **12**: 175–180.

Qian XM, El-Ashker A, Kottke I, Oberwinkler F (1998). Studies of pathogenic and antagonistic microfungal populations and their potential interactions in the mycorrhizoplane of Norway spruce [*Picea abies* (L.) Karst.] and beech (*Fagus sylvatica* L.) on acidified and limed plots. *Plant and Soil* **199**: 111–116.

Rasmussen H (1995). *Terrestrial orchids: From seed to mycotrophic plant*. Cambridge University Press, Cambridge, UK.

Read DJ (1974). *Pezizella ericae* sp. nov., the perfect state of a typical mycorrhizal endophyte of *Ericaceae*. *Transactions of the British Mycological Society* **63**: 381–383.

Read DJ (1991). Mycorrhizas in ecosystems. *Experientia* **47**: 376–391.

Read DJ (2002). Towards ecological relevance – progress and pitfalls in the path towards an understanding of mycorrhizal functions in nature. In: van der Heijden MGA, Sanders IR (eds) *Ecological Studies, vol 157. Mycorrhizal Ecology*. Springer-Verlag, Berlin. pp. 1–29.

Rice AV, Currah RS (2001). Physiological and morphological variation in *Oidiodendron maius*. *Mycotaxon* **79**: 383–396.

Rice AV, Currah RS (2002). New perspectives on the niche and holomorph of the myxotrichoid hyphomycete, *Oidiodendron maius*. *Mycological Research* **106**: 1463–1467.

Rice AV, Currah RS (in press). *Oidiodendron*: A survey of the named species and related anamorphs of *Myxotrichum*. *Studies in Mycology* (accepted Feb. 2005).

Robak H (1932). Investigations regarding fungi on Norwegian ground woodpulp and fungal infections at woodpulp mills. *Saertrykk av Nyt Magazin for Naturvidenskaberne* **71**: 185–330.

Roose-Amsaleg C, Brygoo Y, Harry M (2004). Ascomycete diversity in soil-feeding termite nests and soils from a tropical rainforest. *Environmental Microbiology* **6**: 462–469.

Schild DE, Kennedy A, Stuart MR (1988). Isolation of symbiont and associated fungi from ectomycorrhizas of Sitka spruce. *European Journal of Forest Pathology* **18**: 51–61.

Seiber TN (2002). Fungal root endophytes. In: Wasel Y, Eshel A, Kafkafi U (eds.) *Plant Roots: The Hidden Half.* Marcel Dekker, New York, USA. pp. 887–917.

Simard SW, Jones MD, Durrall DM (2002). Carbon and nutrient fluxes within and between mycorrhizal plants. In: van der Heijden MGA, Sanders IR (eds) *Ecological Studies, vol 157. Mycorrhizal Ecology*. Springer-Verlag, Berlin. pp. 33–74.

Simon L, Lalonde M, Bruns TD (1992). Specific amplification of the 18S fungal ribosomal genes from VA endomycorrhizal fungi colonizing roots. *Applied Environmental Microbiology* **58**: 291–295.

Smith JE, Molina R, Perry D (1995). Occurrence of ectomycorrhizas on ericaceous and coniferous seedlings grown in soils from the Oregon Coast Range. *New Phytologist* **129**: 73–81.

Smith SE, Read DJ (1997). *Mycorrhizal Symbioses*. 2nd Edition. Academic Press, San Diego, CA, USA.

Starrett MC, Blazich FA, Shafer SR, Grand LF (2001). *In vitro* colonization of micropropagated *Pieris floribunda* by ericoid mycorrhizae. I. Establishment of mycorrhizae on microshoots. *HortScience* **36**: 353–356.

Stoyke G, Currah RS (1991). Endophytic fungi from the mycorrhizae of alpine ericoid plants. *Canadian Journal of Botany* **69**: 347–352.

Sugiyama S, Ohara A, Mikawa T (1999). Molecular phylogeny of onygenalean fungi based on small subunit ribosomal DNA (SSU rDNA) sequences. *Mycoscience* **40**: 251–258.

Summerbell RC (1987). Microfungi associated with the mycorrhizal mantle and adjacent microhabitats within the rhizosphere of black spruce. *Canadian Journal of Botany* **65**: 1085–1095.

Svensson BM (1995). Competition between *Sphagnum fuscum* and *Drosera rotundifolia*: a case of ecosystem engineering. *Oikos* **74**: 205–212.

Thormann MN (2001). *The fungal communities of decomposing plants in southern boreal peatlands of Alberta, Canada*. PhD Dissertation, University of Alberta, Edmonton, AB, Canada.

Thormann MN, Currah RS, Bayley SE (2001). Microfungi isolated from *Sphagnum fuscum* from a southern boreal bog in Alberta. *The Bryologist* **104**: 548–559.

Thormann MN, Currah RS, Bayley SE (2002). The relative ability of fungi from *Sphagnum fuscum* to decompose selected carbon substrates. *Canadian Journal of Microbiology* **48**: 204–211.

Thormann MN, Currah RS, Bayley SE (2004). Patterns of distribution of microfungi in decomposing bog and fen plants. *Canadian Journal of Botany* **82**: 710–720.

Tsuneda A, Currah RS (2004). Ascomatal morphogenesis in *Myxotrichum arcticum* supports the derivation of the *Myxotrichaceae* from a discomycetous ancestor. *Mycologia* **96**: 627–635.

Tsuneda A, Thormann MN, Currah RS (2001). Modes of cell wall degradation of *Sphagnum fuscum* by *Acremonium* cf. *curvulum* and *Oidiodendron maius*. *Canadian Journal of Botany* **79**: 93–100.

Usuki F, Abe JP, Kakishima M (2003). Diversity of ericoid mycorrhizal fungi isolated from hair roots of *Rhododendron obtusum* var. *kaempferi* in a Japanese red pine forest. *Mycoscience* **44**: 97–102.

Vitt DH (1994). An overview of the factors that influence the development of Canadian peatlands. *Memoirs of the Entomological Society of Canada* **169**: 7–20.

Vitt DH, Halsey LA, Thormann MN, Martin T (1996). *Peatland Inventory of Alberta Phase 1: Overview of peatland resources in the natural regions and subregions of the province.* Alberta Peatland Resource Centre, Edmonton, AB, Canada. Publication 96-1.

Von Szilvinyi A (1941). Mikrobiologische Boden untersuchungen im Lunzer Bebiet. *Zentralblatt für Bakteriologie Abietlung II.* **103**: 133–189.

Vrålstad T, Fossheim T, Schumacher T (2000). *Piceirhiza bicolorata* – the ectomycorrhizal expression of the *Hymenoscyphus ericae* aggregate? *New Phytologist* **145**: 549–563.

Vrålstad T, Schumacher T, Taylor AFS (2002). Mycorrhizal synthesis between fungal strains of the *Hymenoscyphus ericae* aggregate and potential ectomycorrhizal and ericoid hosts. *New Phytologist* **153**: 143–152.

Xiao G, Berch S (1992). Ericoid mycorrhizal fungi of *Gaultheria shallon*. *Mycologia* **84**: 470–471.

Xiao G, Berch S (1995). The ability of known ericoid mycorrhizal fungi to form mycorrhizae with *Gaultheria shallon* on forest clearcuts. *Mycologia* **87**: 467–470.

Xiao G, Berch S (1999). Organic nitrogen use by salal ericoid mycorrhizal fungi from northern Vancouver Island and impacts on growth *in vitro* of *Gaultheria shallon*. *Mycorrhiza* **9**: 145–149.

Yang WQ, Goulart BL (2002). Mycorrhizal infection reduces short-term aluminum uptake and increases root cation exchange capacity of highbush blueberry plants. *HortScience* **35**: 1083–1086.

Yang WQ, Goulart BL, Demchak K (1998). Mycorrhizal infection and plant growth of highbush blueberry in fumigated soil following soil amendment and inoculation with mycorrhizal fungi. *HortScience* **33**: 1136–1137.

Yang WQ, Goulart BL, Demchak K (2002). Interactive effects of mycorrhizal inoculation and organic soil amendments on nitrogen acquisition and growth of highbush blueberry. *Journal of the American Society of Horticultural Science* **127**: 742–748.

Zhang Y-H, Zhuang w-Y 92004). Phylogenetic relationships of some members in the genus *Hymenoscyphus* (*Ascomycetes, Helotiales*). *Nova Hedwigia* **78**: 475–484.

CHAPTER 8: CONCLUSIONS AND FUTURE DIRECTIONS

Peatlands are important global carbon stores because of the extremely slow decomposition of their vegetation and anything that affects the rates of decay can have serious consequences for the global carbon cycle. Fungi are likely the most important decomposers of peat and knowledge of their diversity, biology, and ecology in peatlands is critical for understanding decomposition processes and the potential effects of climate and environmental changes. Peat is high in cellulose and phenolic compounds and fungi that are able to decompose these materials are likely abundant and important components of the decomposer community in peatlands. The original objective of this study was to isolate selectively the lignocellulose decomposer fungi from *Sphagnum* L. peat and to determine the effects of temperature on their ecology. The most abundant group of lignocellulose degrading fungi isolated was the ascomycete family *Myxotrichaceae*. Most members of this family are psychrophilic or psychrotolerant and show growth inhibition at temperatures above 20°C. The taxonomy, biology, and ecology of this group are poorly understood and the focus of the study shifted to improve our understanding of the taxonomy and basic biology of this group of fungi and to determine their potential ecological roles in *Sphagnum* peatlands. Many other groups of fungi have been isolated from peatlands, including species of *Penicillium* Link, and similar research is needed to understand their biology and determine their roles in peatlands. My research on the *Myxotrichaceae* can best be seen as a case study on peatland fungi.

8.1 Myxotrichaceae in Peatlands

The *Myxotrichaceae* includes three teleomorph genera (*Myxotrichum* Kunze, *Gymnostellatospora* Udagawa, Uchiyama & Kamiya, *Pseudogymnoascus* Raillo) and their anamorphs in *Oidiodendron* Robak and *Geomyces* Traaen (Sigler *et al.* 2000). The teleomorph taxa are rare and none had been reported previously from peat. The anamorph taxa are common saprobes and *Oidiodendron* species have been reported previously from peat (Barron 1962, Nilsson *et al.* 1992, Thormann *et al.* 2001, 2004a) and *Geomyces* species have been reported previously from many substrates, including bryophytes, in cold and temperate environments (e.g. Del Frate & Caretta 1990, Kerry 1990, Mercantini *et al.* 1993, Möller & Dreyfuss 1996, Azmi & Seppelt 1998, Marshall 1998, Sigler & Flis 1998, Bergero *et al.* 1999). The family can be divided into two lineages, the first comprising *Oidiodendron* and *Myxotrichum* and the second comprising *Gymnostellatospora*, *Pseudogymnoascus*, and *Geomyces* (Mori *et al.* 2000, Sigler *et al.* 2000).

Representatives of the first lineage were reported previously from peat but until my study, the second lineage was unknown from this substrate.

Representatives of both lineages of the Myxotrichaceae were common in peat samples and from lignocellulose rich bait blocks placed in the *Sphagnum* bog. *Oidiodendron maius* Barron was the most commonly observed species on moist-incubated peat fragments (Rice & Currah 2002) and it, along with five other species of *Oidiodendron*, was common on moist-incubated bait blocks. *Oidiodendron griseum* Robak, *O. periconioides* Morrall, *O. rhodogenum* Robak and two unidentified species were also isolated from the bait blocks, bringing to 13 the total number of *Oidiodendron* species from peat, making it the seventh most diverse ascomycete genus from peat (Thormann, in press 1). The *Geomyces pannorum* (Link) Sigler & Carmichael complex was overall the most commonly observed taxon on bait blocks and among the most common taxa on peat fragments. It was the most common taxon on peat fragments and bait blocks incubated on mycosel agar and on moist-incubated bait (Chapter 6). It was more common than any non-myxotrichaceous fungi on moist incubated peat fragments. Several *Geomyces* isolates from the bait blocks produced teleomorphs in pure culture. These isolates represented two novel species of *Pseudogymnoascus* and are the first teleomorph-based reports of *Myxotrichaceae* from peat.

8.2 Taxonomic Considerations

Historically, the genera in the *Myxotrichaceae* were included with other cleistothecial ascomycetes with arthroconidial anamorphs in the order *Onygenales* (Currah 1985) but molecular evidence indicated that cleistothecia and arthroconidia were not taxonomically reliable at the ordinal level and that the *Myxotrichaceae* was more closely related to the inoperculate discomycetes in the *Leotiomycetes* (Sugiyama *et al.* 1999, Mori *et al.* 2000, Gibas *et al.* 2002). Molecular evidence has also revealed two distinct lineages within the family (Mori *et al.* 2000) although the exact relationship between them is uncertain.

Within each genus, most taxonomic research has focused on morphological characters (e.g. Barron 1962, Carmichael 1962, Sigler & Carmichael 1976, van Oorschot 1980, Currah 1985, Udagawa *et al.* 1993, Udagawa 1997, Sigler *et al.* 2000) but, except for *Oidiodendron* (Hambleton & Currah 1997, Hambleton *et al.* 1998, Lacourt *et al.* 2001, Sigler & Gibas, in press), the reliability of these characters has not been tested using DNA sequence comparisons.

In *Oidiodendron*, species were traditionally distinguished on the basis of colony morphology, conidiophore length, and conidial dimensions and colour (e.g. Barron 1962, Ellis 1971, 1976, Domsch *et al.* 1980) but ITS sequence data suggest that these characters may be unreliable for some species (Hambleton & Currah 1997, Hambleton *et al.* 1998, Lacourt *et al.* 2001). Additional morphological characters, including conidiophore branching and ornamentation, and conidial shape and ornamentation, and physiological characters, including enzyme profiles, and pH and temperature optima, were more reliable than conidiophore length and conidial dimensions (Chapter 4). A new species, *Oidiodendron fimicolum* Rice & Currah, was described from material obtained from mushroom compost (Chapter 3), *O. fuscum* Robak was reestablished as the type of the genus, *O. citrinum* Barron was transferred to *O. maius* as *O. maius* var. *citrinum* Rice & Currah, *O. scytaloides* Gams & Söderström, *O. reticulatum* Calduch, Stchigel, Gené & Guarro, and *O. ramosum* Calduch, Stchigel, Gené & Guarro were synonymized with *O. chlamydosporicum* Morrall, *O. hughesii* Udagawa & Uchiyama, and *O. setiferum* Udagawa & Toyazaki respectively, and two species, *O. robustum* Mercado Sierra & Casteñeda Ruiz and *O. terrestre* Roy & Singh were excluded (Chapter 4). Dichotomous and synoptic keys were provided to 23 species (Chapter 4) and Biolog FF plates were shown to have potential for rapidly identifying *O. fimicolum, O. maius, O. truncatum* Barron, *O. rhodogenum, O. periconioides,* and an unidentified species from Perryvale Bog although more research will be necessary to establish a database of Biolog profiles for routine identification of *Oidiodendron* species (Chapter 3).

Pseudogymnoascus and *Gymnostellatospora* have traditionally been distinguished based on ascospore ornamentation and the presence of *Geomyces* anamorphs, with species of *Pseudogymnoascus* having smooth ascospores and *Geomyces* anamorphs while species of *Gymnostellatospora* have ornamented ascospores and lack *Geomyces* anamorphs (Udagawa *et al.* 1993, Uchiyama *et al.* 1995, Udagawa 1997, Sigler *et al.* 2000, Udagawa & Uchiyama 2000). *Pseudogymnoascus appendiculatus* Rice & Currah and *P. verrucosus* Rice & Currah were described from Perryvale Bog and both species have ornamented ascospores and *Geomyces* anamorphs, characters that appeared intermediate to *Pseudogymnoascus* and *Gymnostellatospora* (Chapter 5), supporting a previous hypothesis (Sigler *et al.* 2000) that the two genera may exist along a continuum and prompting a phylogenetic reevaluation of the genera and some *Geomyces* species. ITS sequence data indicated that the two new species were distinct from each other and from *Pseudogymnoascus roseus* Raillo and that the three *Pseudogymnoascus* species formed a monophyletic clade that also included several *Geomyces* isolates. This clade was distinct from another monophyletic clade that included all sequenced *Gymnostellatospora* species and *Geomyces asperulatus* Sigler & Carmichael. Thus, the two genera are retained and can be distinguished on the basis of ascospore ornamentation alone. *Gymnostellatospora* species have ascospores with longitudinal bands and striations while those of the *Pseudogymnoascus* species lack striations and are smooth to irregularly ornamented or with a single faint longitudinal band. The relationships among *Gymnostellatospora* species were not well resolved and multiple isolates of most of the species need to be tested to confirm their relationships and monophyly. The presence of *Geomyces* species in both clades and as an outgroup indicates that the genus is polyphyletic (Chapter 5) and that *G. asperulatus* is not a variety of *G. pannorum* as previously suggested (van Oorschot 1980). Additional morphological, physiological, and molecular testing of more isolates of *Geomyces* species is necessary to clarify species concepts and relationships within the genus.

8.3 Potential Ecological Roles

The abundance of *Myxotrichaceae* in the peat and bait suggests that they are common in the substrate in nature and that they are probably playing an ecologically significant role. Most *Myxotrichaceae* are cellulolytic and it is likely that they are degrading cellulose-rich peat. However, as evidenced by enzyme profiling for taxonomy, members of this family also degrade a variety of other plant, animal, and fungal derived compounds, including pectin, starch, tannic acid, chitin, gelatin, lipids and in some cases lignin (Rice & Currah 2001, Thormann *et al.* 2002, Chapter 4) and may be capable of degrading fungal, plant, and animal remains within the peat. Previous studies have shown that *Oidiodendron maius* (Piercey *et al.* 2002, Thormann *et al.* 2002) and *O. chlamydosporicum* (Thormann *et al.* 2002) can cause mass losses of *Sphagnum* that were comparable to or greater than those caused by other saprobic (Thormann *et al.* 2002) or mycorrhizal (Piercey *et al.* 2002) fungi and that *O. maius* can degrade all of the cell wall components of *Sphagnum* leaves (Tsuneda *et al.* 2001). The ability to degrade cellulose is widespread in both lineages of the family (e.g. Currah 1985, Dalpé 1991, Udagawa *et al.* 1993, Uchiyama *et al.* 1995, Sigler *et al.* 2000, Udagawa & Uchiyama 2000, Chapters 4, 6) and species in both lineages are also able to degrade soluble phenolics, including tannic acid (Bending & Read 1996, 1997, Thormann *et al.* 2002, Chapters 4,6) and the ability to degrade *Sphagnum* peat is also likely to be widespread. All nine myxotrichaceous species isolated from Perryvale Bog were able to cause mass loss of *Sphagnum*, although the species and individual isolates of species varied in the percentage of mass loss they caused. Percentages ranged from negligible to approximately 50% over 16 weeks with means of approximately 15% for most species. *Oidiodendron periconioides* caused the highest mass losses. Regardless of the amount of mass loss caused by each species, they all eroded the *Sphagnum* leaf cell walls in the same manner, removing all of the cell wall components more or less simultaneously to leave localized voids adjacent to hyphae. This pattern is analogous to simultaneous white rot of wood. The enzymatic abilities and pattern of degradation observed for the *Myxotrichaceae* differed slightly from those observed in two white-rot basidiomycetes, although the two groups caused similar amounts of mass loss. The basidiomycetes, *Bjerkandera adusta* (Wildenow) Karsten and *Phanerochaete chrysosporium* Burdsall, degraded cellulose and insoluble phenolics but not soluble phenolics, and preferentially removed the polyphenolic matrix to expose the cellulose microfibrils in the *Sphagnum* cell walls, a pattern analogous to preferential white rot of wood. The results of these enzyme assays and decomposition studies indicate that members of the *Myxotrichaceae* have the potential to degrade *Sphagnum* and other components of the peat and may be important saprobes in this environment. In peatlands, slow decomposition limits carbon release and nutrient availability for plants, so it follows that fungi that can decompose *Sphagnum* are important in nutrient cycling and productivity.

The importance of *Myxotrichaceae* in nutrient cycling and productivity in peatlands may be greater than that of other saprobes because at least some of the species may form mycorrhizal associations with the dominant vascular plants and, thus, supply nutrients directly to their hosts. *Oidiodendron maius* is known to form *in situ* ericoid mycorrhizal associations with a variety of ericaceous shrubs (e.g. Douglas *et al.* 1989, Perotto *et al.* 1996, Hambleton & Currah 1997, Currah *et al.* 1999, Chambers *et al.* 2000, Usuki *et al.* 2003) and it was the most frequently observed species on moist incubated peat fragments, appearing in all but one of 288 moist chambers, suggesting that it is present throughout the peat. Presumably, it is growing through the peat, decomposing *Sphagnum* and other constituents of the peat and transferring some of the nutrients, and possibly carbon, back to its hosts (Chapter 7). Other *Oidiodendron* species, including *O. periconioides* (Dalpé 1986, 1991, Currah *et al.* 1993), *O. rhodogenum* (Dalpé 1986, 1991), and *O. griseum* (e.g. Pearson & Read 1973, Couture *et al.* 1983, Dalpé 1986, 1991, Stoyke & Currah 1991, Xiao & Berch 1992), isolated from Perryvale Bog, and *Pseudogymnoascus roseus* (Dalpé 1989), a close relative of the two *Pseudogymnoascus* species isolated from the bog, also form ericoid mycorrhizal associations under certain conditions. Several myxotrichaceous species have also been isolated from ectomycorrhizal root tips (Schild *et al.* 1988, Perotto *et al.* 1995, Qian *et al.* 1998, Sigler & Flis 1998) and they along with other ericoid mycorrhizal fungi may form three-way associations with ectomycorrhizal trees and ericoid mycorrhizal shrubs (Summerbell *et al.* 1987, Perotto *et al.* 1995, Bergero *et al.* 2000, Piercey *et al.* 2002). In these cases, it could be assumed that the fungi would provide nutrients from decomposed peat to both types of host plant. However, it should be noted that *in vitro*, *O. maius* failed to form mycorrhizal associations with either ericaceous shrubs or black spruce when grown in a *Sphagnum* matrix

(Piercey *et al.* 2002) and its presence in both ericaceous and ectomycorrhizal hosts in Perryvale Bog has not been determined.

Mycorrhizal fungi, particularly ericoid and ectomycorrhizal species, can be important decomposers of organic matter in soils (e.g. Bajwa & Read 1985, Read 1991, Northup *et al.* 1995, Bending & Read 1996, 1997, Smith & Read 1997, Aerts 2002, Leake *et al.* 2002, Olsson *et al.* 2002, Simard *et al.* 2002), with the abilities of ericoid mycorrhizal fungi possibly exceeding those of ectomycorrhizal species (Bajwa & Read 1985, Read 1991, Bending & Read 1996, 1997, Smith & Read 1997). In some environments, competition for organic matter between mycorrhizal and non-mycorrhizal fungi reduces the availability of carbon and nutrients for the non-mycorrhizal fungi (Leake *et al.* 2002). In these cases, the decomposition of organic matter by mycorrhizal fungi may be responsible for significant amounts of nutrient and carbon release, and the resultant transfer of this material to host plants may effectively bypass the mineralization step and saprobic community (Leake *et al.* 2002).

8.4 Future Directions

Additional research is still needed to clarify taxonomic relationships among the *Myxotrichaceae* and within several genera in the family. Multiple representatives of the two lineages must be sequenced along with related taxa in the *Leotiomycetes* to determine the precise ordinal placement of the family and to decide whether it should be separated into two distinct families or possibly orders. Relationships among species of *Myxotrichum*, *Gymnostellatospora*, and *Geomyces* need to be resolved. Research on *Myxotrichum* and *Gymnostellatospora* is restricted by the unavailability of living cultures and monotypic nature of many of the species. Numerous isolates of *Geomyces* species are available and should be sequenced in combination with morphological and physiological studies to determine the relationships among taxa and to discover taxonomically informative phenotypic characters that can be used to distinguish them.

More research is also needed into the basic biology of myxotrichaceous fungi. Several species have been reported to form mycorrhizal associations *in vitro* but their presence in these associations in nature has not been confirmed. Selective isolation and culture-free sampling of mycorrhizal roots is needed to determine whether these fungi are present. The functional nature of any associations must also be examined. It has been suggested that these associations may range from parasitic to commensalist to mutualist for both partners and benefits to both the plant and fungus must be investigated. The transfer of carbon and nutrients between the partners should be investigated using radiolabelled carbon, nitrogen, and phosphorus. Growth of the fungi and hosts could be compared in association and on their own to test the effects of the association on the growth and reproduction. *Myxotrichaceae* are typically isolated from soil, wood, and other organic matter where they are assumed to be saprobes, but their saprobic abilities on these substrates are not known. The ability of these fungi to degrade a variety of plant, animal, and fungal-derived substrates, and to cause mass loss and white-rot of *Sphagnum* suggests that they could be important decomposers of plant material, including woody and fungal debris, in soils and decaying logs. This hypothesis should be tested by growing these fungi on target substrates (e.g. wood and mycelium) and assessing mass losses and cell wall erosion.

Other fungi are important in decomposition and nutrient cycling in peatlands. Zygomycetes in the *Mucorales* and hyphomycetes are particularly common in this substrate but their exact roles in decomposition are not known. Mucoralean fungi, in particular, have an uncertain role. These fungi are among the most commonly reported fungi from peat (e.g. Thormann *et al.* 2001, Thormann, in press 1 and 2, Chapter 2, 6) but are adapted to degrade simple carbohydrates rather than the recalcitrant polymers that dominate in peat. It has been suggested, that in addition to degrading simple molecules in the early stages of senescence, these fungi could be subsisting on the byproducts of decomposition of more complex polymers released by other fungi (Thormann, in press 2). Basidiomycetes are not reported frequently from peat, but observations suggest that they are present and that some species are proficient decomposers of the peat. More research is needed to isolate selectively basidiomycetes from peat and to collect and report systematically macrofungi from the bog. Culture-free methods, namely environmental PCR, should be used to determine the relative contribution of basidiomycete mycelium and species diversity to the peat microfungal community. More direct investigation is necessary to determine the roles of different fungi in different stages of peat decay and their contributions to carbon release from peat.

While fungi, with their greater tolerance for acidic conditions, higher biomass and ability to penetrate the substrate, may be the primary decomposers of aerated surface peat, bacteria are also important, particularly in the decomposition of water-logged peat (e.g. Latter *et al.* 1967, Williams & Crawford 1983, Hiroki & Watanabe 1996, Gilbert *et al.* 1998, Dedysh 2002, Thormann *et al.* 2004b). The bacterial community in bogs is not well studied and modern, molecular methods, such as environmental PCR, should be used to sample the bacterial community at different levels in the peat column (Dedysh 2002). The abilities of peatland bacteria to degrade the peat under a variety of environmental conditions should be determined.

Microorganisms, including fungi and bacteria, do not operate alone in decomposition. Different species and groups exist in consortia and positive and negative effects on decomposition may occur due to this synergy. Individual species may facilitate, interfere, or compete with each other. None of these synergistic effects can be determined from *in vitro* studies of individual species or even from microcosm tests using simple, artificial consortia (Thormann *et al.* 2004b). Nevertheless, additional *in vitro* research is probably necessary to determine how different suites of fungi and bacteria interact to decompose peat. Methods should be developed to assess the relative contributions of fungi and bacteria to *in situ* decomposition and to determine the effects of temperature, moisture, and other environmental parameters on fungal and bacterial activities and the resultant release of carbon dioxide and methane from peatlands (Bubier *et al.* 1993, Yavitt *et al.* 1993) since any changes to environmental regimes are likely to destabilize decomposer communities and their interactions.

8.5 Literature Cited

Aerts R (2002). The role of various types of mycorrhizal fungi in nutrient cycling and plant competition. In: van der Heijden MGA, Sanders IR (eds) *Ecological Studies, vol 157. Mycorrhizal Ecology*. Springer-Verlag, Berlin. pp. 117–133.

Azmi OR, Seppelt RD (1998). The broad-scale distribution of microfungi in the Windmill Islands region, continental Antarctica. *Polar Biology* **19**: 92–100.

Bajwa R, Read DJ (1985). The biology of mycorrhiza in the *Ericaceae*. IX. Peptides as nitrogen sources for the ericoid endophyte and for mycorrhizal and non-mycorrhizal plants. *New Phytologist* **101**: 459–467.

Barron GL (1962). New species and new records of *Oidiodendron*. *Canadian Journal of Botany* **40**: 589–607.

Bending GD, Read DJ (1996). Nitrogen mobilization from tannin-protein complexes by ericoid and ectomycorrhizal fungi. *Soil Biology and Biochemistry* **28**: 1603–1612.

Bending GD, Read DJ (1997). Lignin and soluble phenolic degradation by ectomycorrhizal and ericoid mycorrhizal fungi. *Mycological Research* **101**: 1348–1354.

Bergero R, Girlanda MM, Varese GC, Intili D, Luppi AM (1999). Psychrooligotrophic fungi from Arctic soils of Franz Joseph Land. *Polar Biology* **21**: 361–368.

Bergero R, Perotto S, Girlanda MM, Vidano G, Luppi AM (2000). Ericoid mycorrhizal fungi are common root associates of a Mediterranean ectomycorrhizal plant (*Quercus ilex*). *Molecular Ecology* **9**: 1639–1649.

Bubier J, Costello A, Moore TR, Roulet NT, Savage K (1993). Microtopography and methane flux in boreal peatlands, northern Ontario, Canada. *Canadian Journal of Botany* **71**: 1056–1063.

Carmichael JW (1962). *Chrysosporium* and some other aleurosporic hyphomycetes. *Canadian Journal of Botany* **40**: 1137–1173.

Chambers SM, Liu G, Cairney WG (2000). ITS rDNA sequence comparison of ericoid mycorrhizal endophytes from *Woollsia pungens*. *Mycological Research* **104**: 168–174.

Couture M, Fortin JA, Dalpé Y (1983). *Oidiodendron griseum* Robak: an endophyte of ericoid mycorrhiza in *Vaccinium* spp. *New Phytologist* **95**: 375–380.

Currah RS (1985). Taxonomy of the *Onygenales*: *Arthrodermataceae, Gymnoascaceae, Myxotrichaceae* and *Onygenaceae*. *Mycotaxon* **24**: 1–216.

Currah RS, Niemi M, Huhtinen S (1999). *Oidiodendron maius* and *Scytalidium vaccinii* from the mycorrhizas of *Ericaceae* in northern Finland. *Karstenia* **39**: 65–68.

Currah RS, Tsuneda A, Murakami S (1993). Conidiogenesis in *Oidiodendron periconioides* and ultrastructure of ericoid mycorrhizas formed with *Rhododendron brachycarpum*. *Canadian Journal of Botany* **71**: 1481–1485.

Dalpé Y (1986). Axenic synthesis of ericoid mycorrhiza in *Vaccinium angustifolium* Ait. by *Oidiodendron* species. *New Phytologist* **103**: 391–396.

Dalpé Y (1989). Ericoid mycorrhizal fungi in the *Myxotrichaceae* and *Gymnoascaceae*. *New Phytologist* **113**: 523–527.

Dalpé Y (1991). Statut endomycorrhizien du genre *Oidiodendron*. *Canadian Journal of Botany* **69**: 1712–1714.

Dedysh SN (2002). Methanotrophic bacteria of acidic *Sphagnum* peat bogs. *Microbiology* **71**: 638–650.

Del Frate G, Caretta G (1990). Fungi isolated from Antarctic material. *Polar Biology* **11**: 1–7.

Domsch KH, Gams W, Anderson T-H (1980). *Compendium of Soil Fungi*. Academic Press, United Kingdom.

Douglas GC, Heslin MC, Reid C (1989). Isolation of *Oidiodendron maius* from *Rhododendron* and ultrastructural characteristics of synthesized mycorrhizas. *Canadian Journal of Botany* **67**: 2206–2212.

Ellis MB (1971). *Dematiaceous Hyphomycetes*. Commonwealth Agricultural Bureaux, United Kingdom.

Ellis MB (1976). *More Dematiaceous Hyphomycetes*. Commonwealth Agricultural Bureaux, United Kingdom.

Gibas CFC, Sigler L, Summerbell RC, Currah RS (2002). Phylogeny of the genus *Arachnomyces* and its anamorphs and the establishment of *Arachnomycetales*, a new eurotiomycete order in the *Ascomycota*. *Studies in Mycology* **47**: 131–139.

Gilbert D, Amblard C, Bourdier G, Francez A-J (1998). The microbial loop at the surface of a peatland: structure, function, and impact of nutrient input. *Microbial Ecology* **35**: 83–93.

Hambleton S, Currah RS (1997). Fungal endophytes from the roots of alpine and boreal *Ericaceae*. *Canadian Journal of Botany* **75**: 1570–1581.

Hambleton S, Egger KN, Currah RS (1998). The genus *Oidiodendron*: species delimitation and phylogenetic relationships based on nuclear ribosomal DNA analysis. *Mycologia* **90**: 854–869.

Hiroki M, Watanabe MM (1996). Microbial community and rate of cellulose decomposition in peat soils in a mire. *Soil Science and Plant Nutrition* **42**: 893–903.

Kerry E (1990). Microorganisms colonizing plants and soils subjected to different degrees of human activity, including petroleum contamination, in the Vestfold Hills and MacRobertson Land, Antarctica. *Polar Biology* **10**: 423–430.

Lacourt I, Girlanda M, Perotto S, Del Paro M, Zuccon D, Luppi AM (2001). Nuclear ribosomal sequence analysis of *Oidiodendron*: towards a redefinition of ecologically relevant species. *New Phytologist* **149**: 565–576.

Latter PM, Cragg JB, Heal OW (1967). Comparative studies of the microbiology of four moorland soils in the northern Pennines. *Journal of Ecology* **55**: 445–464.

Leake JR, Donnelly DP, Boddy L (2002). Interactions between ecto-mycorrhizal and saprotrophic fungi. In: van der Heijden MGA, Sanders IR (eds) *Ecological Studies, vol 157. Mycorrhizal Ecology*. Springer-Verlag, Berlin. pp. 345–372.

Marshall WA (1998). Aerial transport of keratinaceous substrate and distribution of the fungus *Geomyces pannorum* in Antarctic soils. *Microbial Ecology* **36**: 212–219.

Mercantini R, Marsella R, Moretto D, Finotti E (1993). Keratinophilic fungi in the Antarctic environment. *Mycopathologia* **122**: 169–175.

Möller C, Dreyfuss MM (1996). Microfungi from Antarctic lichens, mosses and vascular plants. *Mycologia* **88**: 922–933.

Mori Y, Sato Y, Takamatsu S (2000). Molecular phylogeny and radiation time of *Erysiphales* inferred from the nuclear ribosomal DNA sequences. *Mycoscience* **41**: 437–447.

Nilsson M, Bååth E, Söderström B (1992). The microfungal communities of a mixed mire in northern Sweden. *Canadian Journal of Botany* **70**: 272–276.

Northup RR, Zengshou Y, Dahlgren RA, Vogt KA (1995). Polyphenol control of nitrogen release from pine litter. *Nature* **377**: 227–229.

Olsson PA, Jakobsen I, Wallander H (2002). Foraging and resource allocation strategies of mycorrhizal fungi in a patchy environment. In: van der Heijden MGA, Sanders IR (eds) *Ecological Studies, vol 157. Mycorrhizal Ecology*. Springer-Verlag, Berlin. pp. 93–115.

Pearson V, Read DJ (1973). The biology of mycorrhiza in *Ericaceae*. I. The isolation of the endophyte and synthesis of mycorrhizas in aseptic culture. *New Phytologist* **72**: 371–379.

Perotto S, Actis-Perino E, Perugini J, Bonfante P (1996). Molecular diversity of fungi from ericoid mycorrhizal roots. *Molecular Ecology* **5**: 123–131.

Perotto S, Perotto R, Faccio A, Schubert A, Varma A, Bonfante P (1995). Ericoid mycorrhizal fungi: cellular and molecular bases of their interactions with the host plant. *Canadian Journal of Botany* **73**: S557–S568.

Piercey MM, Thormann MN, Currah RS (2002). Saprobic characteristics of three fungal taxa from ericalean roots and their association with the roots of *Rhododendron groenlandicum* and *Picea mariana* in culture. *Mycorrhiza* **12**: 175–180.

Qian XM, El-Ashker A, Kottke I, Oberwinkler F (1998). Studies of pathogenic and antagonistic microfungal populations and their potential interactions in the mycorrhizoplane of Norway spruce [*Picea abies* (L.) Karst.] and beech (*Fagus sylvatica* L.) on acidified and limed plots. *Plant and Soil* **199**: 111–116.

Read DJ (1991). Mycorrhizas in ecosystems. *Experientia* **47**: 376 – 391.

Rice AV, Currah RS (2001). Physiological and morphological variation in *Oidiodendron maius*. *Mycotaxon* **79**: 383–396.

Rice AV, Currah RS (2002). New perspectives on the niche and holomorph of the myxotrichoid hyphomycete, *Oidiodendron maius*. *Mycological Research* **106**: 1463–1467.

Rice AV, Currah RS (in press 1). *Oidiodendron*: A survey of the named species and related anamorphs of *Myxotrichum*. *Studies in Mycology* (accepted Feb. 2005).

Rice AV, Currah RS (in press 2). Profiles from Biolog FF plates and morphological characteristics support the recognition of *Oidiodendron fimicolum* sp. nov. *Studies in Mycology* (accepted March 2005).

Rice AV, Currah RS (in press 3). *Oidiodendron maius*: Saprobe in *Sphagnum* peat, mutualist in ericaceous roots? In: Schulz B, Boyle C, Sieber T (eds) *Microbial Root Endophytes*. Springer-Verlag, Heidelberg (Accepted Jan. 2005).

Schild DE, Kennedy A, Stuart MR (1988). Isolation of symbiont and associated fungi from ectomycorrhizas of Sitka spruce. *European Journal of Forest Pathology* **18**: 51–61.

Sigler L, Carmichael JW (1976). Taxonomy of *Malbranchea* and some other hyphomycetes with arthroconidia. *Mycotaxon* **4**: 349–488.

Sigler L, Flis A (1998). *Catalogue of the University of Alberta Microfungus Collections and Herbarium*, 3rd Edition. University of Alberta, Edmonton, AB, Canada. (available online at www.devonian.ualberta.ca/uamh)

Sigler L, Gibas CFC (in press). Utility of a cultural method for identification of the ericoid mycobiont *Oidiodendron maius*. *Studies in Mycology*.

Sigler L, Lumley TC, Currah RS (2000). New species and new records of saprophytic ascomycetes (*Myxotrichaceae*) from decaying logs in the boreal forest. *Mycoscience* **41**: 495–502.

Simard SW, Jones MD, Durrall DM (2002). Carbon and nutrient fluxes within and between mycorrhizal plants. In: van der Heijden MGA, Sanders IR (eds) *Ecological Studies, vol 157. Mycorrhizal Ecology*. Springer-Verlag, Berlin. pp. 33–74.

Smith SE, Read DJ (1997). *Mycorrhizal Symbioses*. 2nd Edition. Academic Press, San Diego, CA, USA.

Stoyke G, Currah RS (1991). Endophytic fungi from the mycorrhizae of alpine ericoid plants. *Canadian Journal of Botany* **69**: 347–352.

Sugiyama S, Ohara A, Mikawa T (1999). Molecular phylogeny of onygenalean fungi based on small subunit ribosomal DNA (SSU rDNA) sequences. *Mycoscience* **40**: 251–258.

Summerbell RC (1987). Microfungi associated with the mycorrhizal mantle and adjacent microhabitats within the rhizosphere of black spruce. *Canadian Journal of Botany* **65**: 1085–1095.

Thormann MN (in press 1). Diversity and function of fungi in peatlands: A carbon cycling perspective. *Canadian Journal of Soil Science*. (Accepted Mar. 2005).

Thormann MN (in press 2). The role of fungi in decomposition dynamics in peatlands. In: Vitt DH, Wieder RK (eds) *Boreal Peatlands*. Springer-Verlag, Berlin. (Accepted Mar. 2005).

Thormann MN, Bayley SE, Currah RS (2004b). Microcosm tests of the effects of temperature and microbial species number on the decomposition of *Carex aquatilus* and *Sphagnum fuscum* litter from southern boreal peatlands. *Canadian Journal of Microbiology* **50**: 793–802.

Thormann MN, Currah RS, Bayley SE (2001). Microfungi isolated from *Sphagnum fuscum* from a southern boreal bog in Alberta. *The Bryologist* **104**: 548–559.

Thormann MN, Currah RS, Bayley SE (2002). The relative ability of fungi from *Sphagnum fuscum* to decompose selected carbon substrates. *Canadian Journal of Microbiology* **48**: 204–211.

Thormann MN, Currah RS, Bayley SE (2004a). Patterns of distribution of microfungi in decomposing bog and fen plants. *Canadian Journal of Botany* **82**: 710–720.

Tsuneda A, Thormann MN, Currah RS (2001). Modes of cell wall degradation of *Sphagnum fuscum* by *Acremonium* cf. *curvulum* and *Oidiodendron maius*. *Canadian Journal of Botany* **79**: 93–100.

Uchiyama S, Kamiya S, Udagawa S (1995). Five onygenalean fungi from Japan. *Mycoscience* **36**: 211–220.

Udagawa S (1997). Taxonomic studies on Plectomycetes (cleistothecial ascomycetes). *Transactions of the Mycological Society of Japan* **38**: 143–157.

Udagawa S, Uchiyama S (2000). Two onygenalean fungi from Russian Far East soil. *Mycoscience* **41**: 217–221.

Udagawa S, Uchiyama S, Kamiya S (1993). *Gymnostellatospora*, a new genus of the *Myxotrichaceae*. *Mycotaxon* **48**: 157–164.

Usuki F, Abe JP, Kakishima M (2003). Diversity of ericoid mycorrhizal fungi isolated from hair roots of *Rhododendron obtusum* var. *kaempferi* in a Japanese red pine forest. *Mycoscience* **44**: 97–102.

Van Oorschot CAN (1980). A revision of *Chrysosporium* and allied genera. *Studies in Mycology* **20**: 1–89.

Williams RT, Crawford RL (1983). Microbial diversity of Minnesota peatlands. *Microbial Ecology* **9**: 201–214.

Xiao G, Berch S (1992). Ericoid mycorrhizal fungi of *Gaultheria shallon*. *Mycologia* **84**: 470–471.

Yavitt JB, Wieder RK, Lang GE (1993). CO_2 and CH_4 dynamics of a *Sphagnum*-dominated peatland in West Virginia. *Global Biogeochemical Cycles* **7**: 259–274.

APPENDIX 1: BIOLOG FF (FILAMENTOUS FUNGI) SUBSTRATES

Well	Substrate	Well	Substrate
A1	Water	E1	D-ribose
A2	Tween 80	E2	Salicin
A3	N-acetyl-D-galactosamine	E3	Sedoheptulosin
A4	N-acetyl-D-glucosamine	E4	D-sorbitol
A5	N-acetyl-D-mannosamine	E5	L-sorbose
A6	Adonitol	E6	Stachyose
A7	Amygdalin	E7	Sucrose
A8	D-arabinose	E8	D-tagatose
A9	L-arabinose	E9	D-trehalose
A10	D-arabitol	E10	Turanose
A11	Arbutin	E11	Xylitol
A12	D-cellobiose	E12	D-xylose
B1	a-cyclodextrin	F1	y-amino-butyric acid
B2	B-cyclodextrin	F2	bromosuccinic acid
B3	Dextrin	F3	Fumaric acid
B4	i-erythritol	F4	B-hydroxy-butyric acid
B5	D-fructose	F5	y-hydroxy-butyric acid
B6	L-fructose	F6	p-hydroxphenyl-acetic acid
B7	D-galactose	F7	a-keto-glutaric acid
B8	D-galacturonic acid	F8	D-lactic acid methyl ester
B9	Gentiobiose	F9	D-lactic acid
B10	D-gluconic acid	F10	D-malic acid
B11	D-glucosamine	F11	L-malic acid
B12	a-D-glucose	F12	Quinic acid
C1	Glucose-1-phosphate	G1	D-saccharic acid
C2	Glucuronamide	G2	Sebacic acid
C3	D-glucuronic acid	G3	Succinamic acid
C4	Glycerol	G4	Succinic acid
C5	Glycogen	G5	Succinic acid mono-methyl ester
C6	m-inositol	G6	N-acetyl-L-glutamic acid

C7	2-keto-D-gluconic acid	G7	Alaninamide
C8	a-D-lactose	G8	L-alanine
C9	Lactulose	G9	L-alanyl-glycine
C10	Maltitol	G10	L-asparagine
C11	Maltose	G11	L-aspartic acid
C12	Maltotriose	G12	L-glutamic acid
D1	D-mannitol	H1	Glycyl-L-glutamic acid
D2	D-mannose	H2	L-ornithine
D3	D-melizitose	H3	L-phenylalanine
D4	D-melibiose	H4	L-proline
D5	a-methyl-D-galactosidase	H5	L-pyroglutamic acid
D6	B-methyl-D-galactosidase	H6	L-serine
D7	a-methyl-D-glucoside	H7	L-threonine
D8	B-methyl-D-glucoside	H8	2-amino ethanol
D9	Palatinose	H9	Putrescine
D10	D-psicose	H10	Adenosine
D11	D-raffinose	H11	Uridine
D12	L-rhamnose	H12	Adenosine 5'-monophosphate

APPENDIX 2: BIOLOG FF PROFILES OF 43 *OIDIODENDRON* AND *MYXOTRICHUM* ISOLATES

Species	Isolate	A1	A2	A3	A4	A5	A6	A7	A8	A9
M. arcticum	UAMH 7565	0	2	0	2	0	0	0	2	2
M. arcticum	UAMH 9243	0	2	2	2	0	2	0	1	2
M. cancellatum	UAMH 1996	0	1	1	2	0	0	0	1	2
M. setosum	UAMH 3835	0	2	0	2	0	2	0	1	2
M. setosum	UAMH 4535	2	2	0	2	0	0	0	0	0
O. cerealis	CBS 349.62	0	1	0	2	0	0	0	0	2
O. cerealis	UAMH 504	0	0	0	2	0	2	0	0	2
O. cerealis	UAMH 1522	0	1	0	2	0	1	0	0	2
O. chlamydosporicum	UAMH 6520	0	2	0	2	0	0	0	1	1
O. chlamydosporicum	UAMH 6521	1	0	0	2	0	0	0	0	1
O. chlamydosporicum	UAMH 9751	0	1	0	2	0	0	0	1	2
O. echinulatum	UAMH 8467	0	1	2	2	0	0	0	1	2
O. fimicolum	UAMH 10459	0	1	0	2	0	0	0	1	2
O. fimicolum	UAMH 10523	0	2	0	2	0	0	0	1	1
O. flavum	UAMH 1524	0	0	0	2	0	2	0	0	2
O. fuscum	UAMH 8511a	0	2	2	2	0	2	0	2	2
O. fuscum	UAMH 8511b	0	2	2	2	0	2	0	0	2
O. griseum	DC 195	0	0	0	2	0	2	0	2	2
O. griseum	UAMH 1403a	0	0	2	0	0	2	0	0	2
O. griseum	UAMH 1403b	0	2	2	2	0	2	1	1	2
O. griseum	UAMH 4080	0	2	2	2	0	2	0	1	2
O. maius var. citrinum	UAMH 1525a	0	0	0	2	0	1	0	1	2
O. maius var. citrinum	UAMH 1525b	0	2	0	2	0	1	0	1	2
O. maius var. citrinum	UAMH 7089	0	2	0	2	0	0	0	1	2
O. maius var. citrinum	UAMH 9275	0	1	0	2	0	0	0	0	2
O. maius var. maius	UAMH 1540a	0	1	0	2	0	0	0	1	2
O. maius var. maius	UAMH 1540b	0	2	0	2	0	1	0	2	2
O. maius var. maius	UAMH 9749	0	2	0	2	0	1	0	2	2
O. periconioides	UAMH 8527	0	2	2	2	2	2	2	2	2
O. periconioides	UAMH 10463	0	2	0	2	0	2	0	2	2
O. periconioides	UAMH 10522	0	2	0	2	0	1	1	2	2
O. pilicola	UAMH 7526	0	2	0	2	0	1	2	2	2

O. rhodogenum	UAMH 1405	0	2	0	2	0	1	0	1	2
O. rhodogenum	UAMH 10462	0	2	0	2	0	0	1	1	2
O. rhodogenum	UAMH 10521	0	2	0	2	0	1	2	2	2
O. setiferum	UAMH 5715a	0	1	0	2	0	1	0	2	2
O. setiferum	UAMH 5715b	0	2	0	2	0	2	0	0	2
O. setiferum	UAMH 5715c	0	2	0	2	0	2	0	0	2
O. tenuissimum	UAMH 1523a	0	2	0	2	0	0	0	1	1
O. tenuissimum	UAMH 1523b	0	2	0	2	0	0	0	1	2
O. tenuissimum	UAMH 1523c	0	2	0	2	0	0	1	1	2
O. tenuissimum	UAMH 8513	0	1	0	2	0	1	0	2	2
O. truncatum	UAMH 1399a	0	0	0	2	0	2	1	2	2
O. truncatum	UAMH 1399b	0	1	0	2	0	2	1	2	2
O. truncatum	UAMH 1399c	0	2	0	2	0	2	1	1	2
O. truncatum	UAMH 1399d	0	1	0	2	0	2	2	1	2
O. truncatum	UAMH 8443	0	1	0	2	0	2	0	2	2
O. truncatum	UAMH 10464a	0	2	0	2	0	2	0	2	2
O. truncatum	UAMH 10464b	0	2	0	2	0	2	0	2	2
Oidiodendron sp. 1	2SMC1-1B	0	2	2	2	0	2	0	0	2
Oidiodendron sp. 1	2SMC5-1A	0	2	1	2	0	2	0	1	2
Oidiodendron sp. 1	3MMC3-7A	0	1	0	2	0	1	0	1	2
Oidiodendron sp. 1	5JyMC2-5A	0	2	2	2	0	2	0	1	2
Oidiodendron sp. 2	4SM3-3	0	2	0	2	0	2	0	2	2

Isolate	A10	A11	A12	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10
UAMH 7565	0	0	2	0	2	2	1	1	0	1	2	2	1
UAMH 9243	1	2	2	0	2	2	2	2	1	2	2	2	0
UAMH 1996	0	2	1	0	1	2	0	2	0	0	2	2	0
UAMH 3835	2	2	2	0	0	2	2	2	0	2	2	2	0
UAMH 4535	2	2	2	0	0	2	2	2	0	2	0	2	0
CBS 349.62	1	2	2	0	1	2	2	2	0	1	1	2	1
UAMH 504	2	2	1	0	2	2	2	2	0	2	2	2	2
UAMH 1522	1	2	2	0	2	2	2	2	0	1	0	2	2
UAMH 6520	2	2	2	0	0	2	2	2	0	1	1	2	0
UAMH 6521	2	2	2	0	1	2	2	1	0	0	2	1	0
UAMH 9751	1	2	2	0	2	2	2	2	0	1	2	2	0
UAMH 8467	2	2	2	1	2	2	2	2	1	2	0	2	2
UAMH 10459	0	1	2	0	0	2	0	2	0	0	0	1	0
UAMH 10523	0	1	2	0	0	2	0	2	0	1	0	2	0
UAMH 1524	2	0	2	0	2	2	2	2	2	2	1	2	0
UAMH 8511a	2	2	2	0	2	2	2	2	2	2	1	2	0
UAMH 8511b	1	2	2	0	1	2	2	2	0	0	0	2	0
DC 195	2	2	2	0	2	2	2	2	0	2	2	2	0
UAMH 1403a	1	2	1	0	2	2	1	1	1	2	2	2	0
UAMH 1403b	2	2	2	0	2	2	2	2	1	2	1	2	1
UAMH 4080	2	2	2	0	2	2	2	2	2	2	1	2	0
UAMH 1525a	1	2	2	0	2	2	0	2	1	2	1	2	0
UAMH 1525b	1	2	2	0	2	2	1	2	1	2	1	2	1
UAMH 7089	0	2	2	0	1	2	0	2	1	1	1	2	0
UAMH 9275	0	2	2	0	2	2	0	2	1	2	0	2	0
UAMH 1540a	0	2	2	0	2	2	0	2	1	2	1	2	0
UAMH 1540b	1	2	2	0	2	2	0	2	2	2	2	2	0
UAMH 9749	1	2	2	0	2	2	0	2	2	2	2	2	0
UAMH 8527	2	0	2	0	2	2	2	2	2	2	2	2	2
UAMH 10463	2	2	2	0	2	2	2	2	2	2	2	2	0
UAMH 10522	2	2	2	0	1	2	2	2	2	2	2	2	0
UAMH 7526	0	2	2	0	0	2	2	2	1	2	2	2	0
UAMH 1405	2	2	2	0	2	2	2	2	1	2	2	2	1
UAMH 10462	2	2	2	0	0	2	2	2	0	2	1	2	0
UAMH 10521	2	2	2	0	1	2	2	2	1	2	2	2	0
UAMH 5715a	1	2	0	0	2	2	2	2	1	2	2	2	1

UAMH 5715b	1	2	2	0	1	2	2	2	0	1	0	2	2
UAMH 5715c	2	2	2	0	2	2	2	2	2	2	0	2	2
UAMH 1523a	0	2	2	0	0	1	1	2	1	1	0	1	0
UAMH 1523b	0	2	2	0	2	2	2	2	1	2	1	2	0
UAMH 1523c	0	2	2	0	2	2	2	2	1	2	2	2	0
UAMH 8513	2	2	2	0	2	2	2	2	1	2	2	2	0
UAMH 1399a	2	2	2	0	0	2	2	2	0	2	2	2	1
UAMH 1399b	2	2	2	0	0	2	2	2	0	2	2	2	1
UAMH 1399c	2	2	2	0	0	2	2	2	0	2	1	2	1
UAMH 1399d	2	2	2	0	0	2	2	2	0	2	1	2	2
UAMH 8443	2	2	2	0	0	2	2	2	0	2	0	2	0
UAMH 10464a	2	2	2	0	0	2	2	2	2	2	2	2	1
UAMH 10464b	2	2	2	0	0	2	2	2	2	2	2	2	2
2SMC1-1B	2	2	2	0	2	2	2	2	1	2	1	2	0
2SMC5-1A	2	2	2	0	2	2	2	2	2	2	2	2	0
3MMC3-7A	1	2	1	0	2	1	2	2	1	2	0	1	0
5JyMC2-5A	2	2	2	0	0	2	2	2	1	2	1	2	0
4SM3-3	2	0	2	0	0	0	1	2	2	2	1	2	2

Isolate	B11	B12	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11
UAMH 7565	2	2	2	0	2	1	2	0	2	2	0	1	2
UAMH 9243	2	1	0	0	2	2	2	0	2	2	1	2	2
UAMH 1996	0	1	0	0	2	0	1	0	2	2	1	1	1
UAMH 3835	1	2	2	0	2	2	0	0	2	2	0	0	2
UAMH 4535	2	2	0	0	2	2	2	0	2	0	0	1	2
CBS 349.62	1	1	2	0	2	2	2	0	0	2	2	2	2
UAMH 504	1	2	2	0	2	2	2	2	2	2	2	2	2
UAMH 1522	0	2	2	0	2	2	2	0	0	2	2	1	2
UAMH 6520	0	2	2	2	1	2	2	1	2	0	0	1	2
UAMH 6521	0	0	2	0	0	2	2	2	2	0	0	0	1
UAMH 9751	2	2	2	0	2	2	2	0	2	2	1	1	2
UAMH 8467	1	2	2	0	2	2	2	0	2	2	2	2	2
UAMH 10459	0	2	0	0	0	0	2	0	0	0	0	0	1
UAMH 10523	0	2	1	0	0	0	2	0	0	0	0	0	1
UAMH 1524	2	2	2	0	2	2	2	2	2	2	2	2	2
UAMH 8511a	2	2	2	0	2	2	2	0	0	2	2	2	2
UAMH 8511b	2	2	2	0	2	2	2	0	0	2	2	2	2
DC 195	2	2	2	0	2	2	2	0	2	2	2	2	2
UAMH 1403a	2	0	2	0	2	2	1	1	2	2	1	2	1
UAMH 1403b	2	2	1	0	2	2	2	1	2	2	1	2	2
UAMH 4080	2	2	2	1	2	2	2	0	2	2	2	2	2
UAMH 1525a	2	2	2	0	2	1	2	2	0	2	2	1	2
UAMH 1525b	2	2	2	0	2	1	2	2	1	2	2	2	2
UAMH 7089	2	2	2	0	2	2	2	2	0	2	2	2	2
UAMH 9275	2	2	2	0	2	1	2	1	0	2	2	0	2
UAMH 1540a	2	2	1	0	2	1	2	1	0	2	2	2	2
UAMH 1540b	2	2	1	0	2	2	2	2	1	2	2	2	2
UAMH 9749	2	2	2	0	2	0	2	1	0	2	2	2	2
UAMH 8527	2	2	0	0	2	2	2	2	2	2	2	2	2
UAMH 10463	2	2	0	0	2	2	2	0	0	2	2	2	2
UAMH 10522	2	2	1	0	2	2	2	0	0	2	1	2	2
UAMH 7526	0	2	2	0	0	2	2	1	0	2	0	0	2
UAMH 1405	2	2	2	0	2	2	2	0	0	2	2	2	2
UAMH 10462	2	2	1	0	2	2	2	0	0	2	2	2	2
UAMH 10521	2	2	1	0	2	2	2	0	0	2	2	2	2
UAMH 5715a	2	1	2	1	2	2	2	0	0	2	2	2	2

UAMH 5715b	2	2	2	0	2	2	2	0	0	2	2	2	2
UAMH 5715c	2	2	2	0	2	2	2	0	0	2	2	2	2
UAMH 1523a	2	2	0	0	0	0	2	0	0	1	0	0	0
UAMH 1523b	2	2	0	0	2	0	2	0	0	2	0	1	2
UAMH 1523c	2	2	0	0	2	1	2	0	0	2	0	2	2
UAMH 8513	2	1	1	0	2	1	2	1	0	2	2	2	2
UAMH 1399a	2	2	2	0	2	2	2	0	2	2	2	2	2
UAMH 1399b	2	2	2	0	2	2	2	0	2	2	2	2	2
UAMH 1399c	2	2	2	0	2	2	2	0	2	2	2	2	2
UAMH 1399d	2	2	2	0	2	2	2	0	2	2	2	1	2
UAMH 8443	2	2	2	0	2	2	2	2	2	2	1	1	2
UAMH 10464a	2	2	2	0	2	2	2	2	2	2	2	2	2
UAMH 10464b	2	2	2	0	2	2	2	2	2	2	2	2	2
2SMC1-1B	2	2	0	0	2	2	2	1	2	2	2	1	2
2SMC5-1A	2	2	2	0	2	2	2	1	2	2	2	1	2
3MMC3-7A	2	1	0	0	2	1	2	0	2	2	2	2	2
5JyMC2-5A	2	2	0	0	2	2	2	1	2	2	2	2	2
4SM3-3	0	2	0	0	2	2	0	1	2	0	1	0	0

Isolate	C12	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10	D11	D12
UAMH 7565	2	2	2	2	1	0	0	1	0	1	1	1	1
UAMH 9243	2	2	2	0	2	0	0	1	2	2	2	2	2
UAMH 1996	2	1	2	0	0	0	0	0	0	1	1	1	1
UAMH 3835	0	2	2	0	1	0	0	0	2	0	1	1	0
UAMH 4535	2	2	2	0	1	1	0	0	2	0	0	0	2
CBS 349.62	2	2	2	0	2	1	1	0	2	2	1	2	1
UAMH 504	2	2	2	2	2	2	2	1	2	2	2	2	2
UAMH 1522	2	2	2	0	2	1	0	0	2	1	0	2	2
UAMH 6520	1	2	2	0	0	0	0	0	2	0	0	2	1
UAMH 6521	1	2	2	0	2	1	2	0	2	1	0	1	0
UAMH 9751	2	2	2	2	2	0	0	1	2	1	0	2	2
UAMH 8467	2	2	2	0	2	1	0	0	2	1	2	2	2
UAMH 10459	1	1	2	0	0	0	0	0	2	0	0	1	1
UAMH 10523	1	1	2	0	1	0	0	0	2	0	0	1	1
UAMH 1524	2	2	2	2	2	0	0	2	2	2	0	2	2
UAMH 8511a	2	2	2	2	2	0	2	0	2	2	0	2	2
UAMH 8511b	2	2	2	2	2	0	2	0	2	2	2	2	2
DC 195	2	2	2	0	2	0	2	2	2	2	0	2	2
UAMH 1403a	1	1	2	2	2	0	0	1	2	1	0	2	1
UAMH 1403b	2	2	2	2	2	0	0	2	2	2	0	1	2
UAMH 4080	2	2	2	2	2	0	0	2	2	2	2	2	2
UAMH 1525a	2	2	2	0	2	0	2	0	2	2	0	2	2
UAMH 1525b	2	2	2	0	2	0	2	1	2	2	1	2	2
UAMH 7089	2	2	2	0	2	0	0	0	2	0	2	2	2
UAMH 9275	2	2	2	0	2	0	1	0	2	0	2	2	2
UAMH 1540a	2	2	2	0	2	0	1	0	2	1	1	2	2
UAMH 1540b	2	2	2	0	2	0	2	0	2	1	1	2	2
UAMH 9749	2	0	2	0	2	0	2	2	0	2	0	2	2
UAMH 8527	2	2	2	2	2	0	2	2	2	2	2	2	2
UAMH 10463	2	2	2	0	2	0	2	2	2	2	2	2	2
UAMH 10522	2	2	2	0	2	0	0	2	2	2	1	2	1
UAMH 7526	2	2	2	1	2	0	0	0	2	0	1	2	2
UAMH 1405	2	2	2	2	2	0	1	0	2	2	2	2	2
UAMH 10462	2	2	2	0	2	0	2	0	2	2	2	2	2
UAMH 10521	2	2	2	2	2	0	2	0	2	2	2	2	2
UAMH 5715a	2	2	2	0	2	0	0	2	0	2	0	2	2

UAMH 5715b	2	2	2	2	2	0	0	2	2	2	2	2	1
UAMH 5715c	2	2	2	2	2	0	2	2	2	2	0	2	2
UAMH 1523a	1	0	2	0	1	0	0	0	2	0	1	2	1
UAMH 1523b	2	1	2	0	2	0	0	1	2	1	1	2	2
UAMH 1523c	2	2	2	0	2	0	0	1	2	2	0	2	2
UAMH 8513	2	2	2	0	2	0	0	2	1	2	0	2	2
UAMH 1399a	2	1	2	0	1	0	0	2	0	2	1	2	2
UAMH 1399b	2	2	2	0	2	0	2	0	2	0	1	2	2
UAMH 1399c	2	2	2	0	2	0	0	0	2	1	2	2	2
UAMH 1399d	2	2	2	0	2	0	0	0	2	0	0	2	2
UAMH 8443	2	2	2	0	2	0	0	1	2	2	0	2	2
UAMH 10464a	2	2	2	0	0	0	0	0	2	2	2	1	2
UAMH 10464b	2	2	2	0	0	0	0	0	2	2	2	2	2
2SMC1-1B	2	2	2	0	2	0	2	0	2	2	2	2	2
2SMC5-1A	2	2	2	0	2	0	2	1	2	2	2	2	2
3MMC3-7A	2	2	1	0	2	0	2	2	1	2	2	2	1
5JyMC2-5A	2	2	2	0	2	0	2	0	2	2	2	2	2
4SM3-3	2	2	2	0	2	2	2	0	2	0	2	2	2

Isolate	E1	E2	E3	E4	E5	E6	E7	E8	E9	E10	E11	E12
UAMH 7565	2	2	0	2	2	2	0	0	2	0	0	2
UAMH 9243	2	2	0	2	2	2	0	0	2	2	1	2
UAMH 1996	2	2	0	0	0	0	0	0	0	0	0	2
UAMH 3835	2	2	0	2	2	0	2	0	2	0	2	2
UAMH 4535	0	0	0	2	2	1	2	0	2	0	0	0
CBS 349.62	2	2	0	2	1	0	0	0	2	2	1	2
UAMH 504	2	2	0	2	2	2	2	0	2	2	2	2
UAMH 1522	1	1	0	2	2	2	2	0	2	2	2	2
UAMH 6520	2	2	0	2	1	1	2	0	2	2	1	2
UAMH 6521	0	2	2	2	2	2	2	2	2	0	0	2
UAMH 9751	2	2	0	2	0	2	2	0	2	2	0	2
UAMH 8467	2	2	2	2	2	2	2	0	2	2	2	2
UAMH 10459	2	1	0	1	0	0	0	0	2	0	0	2
UAMH 10523	2	1	0	1	0	1	1	0	2	0	0	2
UAMH 1524	2	1	0	0	0	2	0	0	2	2	2	2
UAMH 8511a	2	2	0	2	2	2	2	0	2	2	2	2
UAMH 8511b	2	2	0	2	2	2	2	0	2	2	2	2
DC 195	2	2	0	2	2	2	2	0	2	2	2	2
UAMH 1403a	2	0	0	1	1	1	2	0	2	2	2	2
UAMH 1403b	2	2	0	2	2	2	2	0	2	2	2	2
UAMH 4080	2	1	0	2	2	2	0	0	2	2	1	2
UAMH 1525a	2	1	0	2	2	2	2	0	2	1	0	2
UAMH 1525b	2	1	1	2	1	2	2	0	2	2	2	2
UAMH 7089	2	2	0	2	0	2	2	0	2	2	0	2
UAMH 9275	2	1	0	2	2	2	2	0	2	0	2	2
UAMH 1540a	2	2	0	2	2	2	2	0	2	2	1	2
UAMH 1540b	2	2	0	2	2	2	2	0	2	1	2	2
UAMH 9749	2	2	0	2	1	2	2	0	2	1	0	2
UAMH 8527	2	2	2	2	2	2	2	1	2	2	2	2
UAMH 10463	2	2	0	2	2	2	2	1	2	2	2	2
UAMH 10522	2	2	0	2	2	2	2	0	2	2	2	2
UAMH 7526	2	2	0	1	0	2	2	0	2	0	0	2
UAMH 1405	2	2	0	2	2	2	2	0	2	2	2	2
UAMH 10462	2	2	0	2	2	2	0	0	2	2	0	2
UAMH 10521	2	2	0	2	2	2	2	0	2	2	0	2
UAMH 5715a	2	1	0	2	2	2	0	0	2	2	2	2

UAMH 5715b	2	2	0	2	2	2	0	0	2	2	2	2
UAMH 5715c	2	2	0	2	2	2	0	0	2	2	2	2
UAMH 1523a	1	1	0	0	0	1	2	0	0	0	1	2
UAMH 1523b	2	1	0	1	1	2	2	0	2	2	1	2
UAMH 1523c	2	2	0	2	2	2	2	0	2	2	1	2
UAMH 8513	2	1	0	2	0	2	2	0	2	2	0	2
UAMH 1399a	2	2	0	2	2	2	2	1	2	0	0	2
UAMH 1399b	2	2	0	2	2	2	2	0	2	0	0	2
UAMH 1399c	2	2	0	2	2	2	2	0	2	0	0	2
UAMH 1399d	2	2	0	2	2	2	2	0	2	0	0	2
UAMH 8443	2	2	0	2	1	2	2	0	2	0	0	2
UAMH 10464a	2	2	0	2	2	0	2	1	2	1	2	2
UAMH 10464b	2	2	0	2	2	0	2	0	2	2	2	2
2SMC1-1B	2	1	0	2	2	2	2	0	2	0	2	2
2SMC5-1A	2	2	0	2	2	2	2	0	2	0	2	2
3MMC3-7A	2	1	0	2	2	2	2	0	2	0	2	2
5JyMC2-5A	2	2	0	2	2	2	2	0	2	0	2	2
4SM3-3	2	1	0	2	1	2	2	0	2	0	2	2

Isolate	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11	F12
UAMH 7565	1	2	2	2	0	0	2	0	0	2	2	2
UAMH 9243	2	2	2	2	2	0	2	0	2	2	2	2
UAMH 1996	0	0	0	2	0	0	1	0	0	0	0	0
UAMH 3835	0	2	2	0	1	0	2	0	1	2	2	0
UAMH 4535	0	0	0	0	0	0	0	0	0	0	0	0
CBS 349.62	0	1	2	0	2	0	0	0	1	1	2	0
UAMH 504	2	2	2	0	2	2	2	0	2	2	2	2
UAMH 1522	0	0	2	0	2	0	2	0	1	2	2	0
UAMH 6520	1	2	2	2	0	0	2	0	0	2	2	0
UAMH 6521	0	0	1	1	1	0	2	0	0	2	1	2
UAMH 9751	2	1	2	2	0	0	2	0	0	2	2	2
UAMH 8467	1	2	2	2	2	0	2	0	1	2	2	0
UAMH 10459	0	0	1	0	0	0	0	0	0	0	0	2
UAMH 10523	0	0	1	0	0	0	0	0	0	0	0	2
UAMH 1524	2	2	2	2	2	1	2	0	2	2	2	2
UAMH 8511a	2	2	2	2	2	0	2	0	2	2	2	2
UAMH 8511b	2	2	2	2	2	1	2	1	2	2	2	2
DC 195	2	2	2	2	2	0	2	0	2	2	2	2
UAMH 1403a	2	2	2	2	2	0	2	0	1	2	2	2
UAMH 1403b	2	2	2	2	2	0	2	0	2	2	2	2
UAMH 4080	2	2	2	2	1	0	2	2	2	2	2	2
UAMH 1525a	1	1	2	2	2	0	2	0	1	2	2	2
UAMH 1525b	1	2	2	2	2	0	2	0	2	2	2	2
UAMH 7089	2	2	2	2	2	0	2	0	0	2	2	2
UAMH 9275	0	1	2	2	2	0	2	0	1	2	2	2
UAMH 1540a	2	1	2	2	2	0	2	0	0	2	2	2
UAMH 1540b	2	2	2	2	2	0	2	0	1	2	2	2
UAMH 9749	2	2	2	2	0	0	2	0	0	2	2	2
UAMH 8527	0	2	2	1	1	2	0	2	2	2	2	2
UAMH 10463	0	2	2	2	2	0	2	0	0	2	1	0
UAMH 10522	0	2	1	1	2	0	2	0	0	1	1	0
UAMH 7526	0	1	0	2	1	0	1	2	0	1	1	2
UAMH 1405	2	2	2	0	1	0	2	0	1	2	2	0
UAMH 10462	1	2	2	0	0	0	2	0	0	2	2	0
UAMH 10521	1	2	1	1	1	0	2	0	0	2	2	0
UAMH 5715a	2	2	2	1	2	0	2	0	0	2	2	2

UAMH 5715b	2	2	2	2	1	0	2	0	0	2	2	2
UAMH 5715c	2	2	2	2	2	0	2	0	2	2	2	2
UAMH 1523a	0	0	0	2	1	0	1	0	0	0	0	0
UAMH 1523b	1	1	1	2	0	0	1	0	0	1	0	0
UAMH 1523c	2	1	2	2	2	0	2	0	0	2	2	0
UAMH 8513	2	2	2	0	0	0	2	0	1	2	2	2
UAMH 1399a	2	2	2	2	2	2	2	0	0	2	2	2
UAMH 1399b	2	1	2	2	2	2	2	1	0	2	2	2
UAMH 1399c	2	2	2	2	1	2	2	0	1	2	2	2
UAMH 1399d	2	2	2	2	2	2	2	0	1	2	2	2
UAMH 8443	2	2	2	2	2	1	2	0	2	2	2	2
UAMH 10464a	2	2	2	2	2	1	2	0	2	2	2	2
UAMH 10464b	2	2	2	2	2	2	2	1	2	2	2	2
2SMC1-1B	2	2	2	1	2	0	2	0	1	2	2	0
2SMC5-1A	2	2	2	1	2	0	2	0	1	2	2	0
3MMC3-7A	2	2	2	2	2	0	2	0	1	2	2	0
5JyMC2-5A	1	2	2	2	2	0	2	0	1	2	2	1
4SM3-3	2	2	2	2	2	2	2	0	2	2	2	2

Isolate	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	G11	G12
UAMH 7565	2	2	0	2	2	2	2	2	2	2	2	2
UAMH 9243	2	2	2	2	2	2	2	2	2	2	2	2
UAMH 1996	0	0	0	1	2	0	2	2	2	0	2	2
UAMH 3835	0	2	0	2	2	0	1	2	2	2	2	2
UAMH 4535	0	0	0	0	0	0	0	2	0	0	1	2
CBS 349.62	0	2	0	2	2	0	0	2	2	1	2	2
UAMH 504	2	2	2	2	2	0	1	2	2	2	2	2
UAMH 1522	0	2	0	2	2	0	2	2	2	2	2	2
UAMH 6520	0	2	1	2	2	0	1	2	2	0	2	2
UAMH 6521	2	1	0	2	2	0	2	2	2	0	0	1
UAMH 9751	2	2	2	2	2	2	2	2	2	2	2	2
UAMH 8467	0	2	2	2	2	0	2	2	2	2	1	2
UAMH 10459	0	0	0	2	0	0	2	2	2	0	2	2
UAMH 10523	0	0	0	2	0	0	2	2	2	0	2	2
UAMH 1524	2	2	2	2	2	0	2	2	2	2	2	2
UAMH 8511a	0	2	2	2	2	2	2	2	2	2	2	2
UAMH 8511b	0	2	2	2	2	2	2	2	2	2	2	2
DC 195	2	2	2	2	2	0	2	2	2	2	2	2
UAMH 1403a	2	2	1	2	2	2	2	2	2	2	2	2
UAMH 1403b	2	2	2	2	2	2	2	2	2	2	2	2
UAMH 4080	0	2	1	2	2	0	2	2	2	2	2	2
UAMH 1525a	0	2	1	2	2	0	2	2	2	2	2	2
UAMH 1525b	0	2	1	2	2	0	2	2	2	2	2	2
UAMH 7089	0	2	1	2	2	0	2	2	2	2	2	2
UAMH 9275	0	2	2	2	2	0	2	2	2	2	2	2
UAMH 1540a	0	2	0	2	2	0	1	2	1	1	2	2
UAMH 1540b	0	2	2	2	2	0	2	2	2	2	2	2
UAMH 9749	0	2	1	2	2	2	0	2	1	1	2	2
UAMH 8527	0	2	2	2	2	2	0	2	2	1	2	2
UAMH 10463	0	2	2	2	2	0	2	2	1	0	0	2
UAMH 10522	0	2	1	1	2	0	2	2	2	0	1	2
UAMH 7526	0	1	2	2	2	0	2	2	1	2	0	0
UAMH 1405	0	2	2	2	2	0	2	2	2	2	1	2
UAMH 10462	0	2	1	2	2	0	2	2	2	2	1	2
UAMH 10521	0	2	1	2	2	0	1	2	2	2	2	2
UAMH 5715a	0	2	1	2	2	2	2	2	2	2	2	2

UAMH 5715b	0	2	2	2	2	2	2	2	2	2	2	2
UAMH 5715c	0	2	2	2	2	2	2	2	2	2	2	2
UAMH 1523a	0	2	2	0	2	1	2	2	2	1	1	2
UAMH 1523b	0	2	2	2	2	2	2	2	2	2	2	2
UAMH 1523c	0	2	2	2	2	2	2	2	2	2	2	2
UAMH 8513	2	2	2	2	2	2	2	2	2	2	2	2
UAMH 1399a	0	2	2	2	2	2	2	2	2	2	2	2
UAMH 1399b	0	2	2	2	2	1	2	2	2	2	2	2
UAMH 1399c	0	2	2	2	2	0	2	2	2	2	2	2
UAMH 1399d	0	2	2	2	2	0	2	2	2	2	2	2
UAMH 8443	0	2	2	2	0	0	2	2	2	2	2	2
UAMH 10464a	0	2	2	2	2	1	2	2	2	2	2	2
UAMH 10464b	0	2	2	2	2	2	2	2	2	2	2	2
2SMC1-1B	2	2	0	2	2	2	2	2	2	2	2	2
2SMC5-1A	2	2	1	2	2	2	2	2	2	2	2	2
3MMC3-7A	2	2	1	2	2	2	2	2	2	2	2	2
5JyMC2-5A	2	2	1	2	2	0	2	2	2	2	1	2
4SM3-3	2	2	2	2	2	2	2	2	2	2	2	2

Isolate	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	H12
UAMH 7565	2	2	2	2	2	2	2	0	0	0	0	0
UAMH 9243	2	2	2	2	2	2	2	0	2	0	1	0
UAMH 1996	2	2	1	2	2	2	2	1	0	0	0	0
UAMH 3835	2	0	0	2	2	2	0	0	0	0	1	0
UAMH 4535	0	2	0	2	2	2	2	0	0	0	0	0
CBS 349.62	2	2	2	2	0	0	0	0	0	0	0	0
UAMH 504	0	2	2	2	2	2	1	0	0	0	0	0
UAMH 1522	2	2	2	2	2	2	2	0	1	0	0	0
UAMH 6520	0	2	2	2	0	2	0	0	0	0	0	0
UAMH 6521	2	2	2	2	0	2	2	2	2	0	2	2
UAMH 9751	2	2	2	2	2	2	2	0	1	0	0	0
UAMH 8467	1	2	2	2	2	2	1	0	0	0	0	0
UAMH 10459	2	0	0	2	2	2	0	0	0	0	0	0
UAMH 10523	2	0	0	2	2	2	0	0	0	0	0	0
UAMH 1524	2	2	2	2	0	2	2	0	0	0	0	0
UAMH 8511a	2	2	2	2	2	2	2	2	2	0	0	0
UAMH 8511b	2	2	2	2	2	2	2	2	2	0	0	2
DC 195	2	2	2	2	2	2	2	0	2	0	0	0
UAMH 1403a	2	2	2	2	2	2	2	1	2	0	1	0
UAMH 1403b	2	2	2	2	2	2	2	0	2	0	0	0
UAMH 4080	2	2	2	2	2	2	2	0	1	0	1	1
UAMH 1525a	2	2	2	2	2	2	2	0	0	0	0	0
UAMH 1525b	2	2	2	2	2	2	2	0	0	1	0	0
UAMH 7089	2	2	2	2	2	2	2	0	0	0	0	0
UAMH 9275	2	2	2	2	2	2	2	0	0	0	0	0
UAMH 1540a	2	1	2	2	2	2	1	0	0	0	0	0
UAMH 1540b	2	2	2	2	2	2	2	0	0	0	0	0
UAMH 9749	0	1	2	2	2	2	0	0	0	0	0	0
UAMH 8527	2	0	0	2	2	0	0	0	0	2	0	0
UAMH 10463	0	0	2	2	2	2	0	0	0	0	0	0
UAMH 10522	0	0	2	2	2	1	0	0	0	0	0	0
UAMH 7526	0	2	2	0	0	0	1	2	2	1	2	0
UAMH 1405	2	2	2	2	2	2	2	0	0	1	0	0
UAMH 10462	2	1	2	2	1	2	2	0	0	0	0	0
UAMH 10521	2	1	2	2	2	2	2	0	0	0	0	0
UAMH 5715a	2	2	2	2	2	2	2	0	2	0	0	0

UAMH 5715b	2	2	2	2	2	2	2	0	1	0	0	0
UAMH 5715c	2	2	2	2	2	2	2	0	2	0	0	0
UAMH 1523a	2	0	1	1	1	2	2	0	0	0	0	0
UAMH 1523b	1	1	1	2	2	2	2	0	0	0	0	0
UAMH 1523c	2	2	2	2	2	2	2	0	0	0	0	0
UAMH 8513	2	2	2	2	2	2	2	0	0	0	0	0
UAMH 1399a	0	2	2	2	2	2	2	2	2	0	0	0
UAMH 1399b	2	2	2	2	2	2	2	2	2	0	0	0
UAMH 1399c	2	2	2	2	2	2	2	1	2	0	0	0
UAMH 1399d	0	2	2	2	2	2	2	2	2	1	0	1
UAMH 8443	2	2	2	2	2	2	2	2	2	0	0	0
UAMH 10464a	2	2	2	2	2	2	2	2	2	0	0	0
UAMH 10464b	2	2	2	2	2	2	2	2	2	0	0	0
2SMC1-1B	2	2	2	2	2	2	2	0	2	0	0	0
2SMC5-1A	1	2	2	2	2	2	2	0	2	0	0	0
3MMC3-7A	0	2	2	2	2	2	2	0	2	0	0	0
5JyMC2-5A	0	2	2	2	2	2	2	0	2	0	0	0
4SM3-3	2	2	2	2	2	2	2	1	2	2	2	2

APPENDIX 3: ACCESSION INFORMATION FOR *MYXOTRICHACEAE* DEPOSITED AT THE UNIVERSITY OF ALBERTA MICROFUNGUS COLLECTION AND HERBARIUM (UAMH)

Species	Collection Number	UAMH Number
Oidiodendron fimicolum	DC 60[a]	10459[t]
Oidiodendron fimicolum	DC 61[a]	10523
Oidiodendron maius	S4-P3-P-4[b]	10460
Oidiodendron maius	F-02[c]	10461
Oidiodendron maius	S1-P6-C-1[b]	10508
Oidiodendron periconioides	3AMC4-10A	10463
Oidiodendron periconioides	1JyMC5-7A	10522
Oidiodendron rhodogenum	4SMC1-5	10462
Oidiodendron rhodogenum	5AMC4-9	10521
Oidiodendron truncatum	H682[d]	10464
Pseudogymnoascus appendiculatus	3SMC4-3	10509[t,h]
Pseudogymnoascus appendiculatus	3SMC1-3	10510
Pseudogymnoascus appendiculatus	3SMC5-2	10511
Pseudogymnoascus appendiculatus	2JnM5-1	10512
Pseudogymnoascus verrucosus	4JyM1-2	10579[t,h]
Pseudogymnoascus verrucosus	4JyM4-1	10580[p]

[a] Sender: DC = Pennsylvania State Mushroom Spawn Laboratory, [b] Collector: Grace Hill-Rackette, [c] Collector: Randolph Currah, [d] Collector: Trevor Lumley

[t] *ex*-type culture, [h]holotype specimen, [p]*ex*-paratype culture

APPENDIX 4: GLOSSARY OF TERMS

This glossary contains terms used in this thesis. Definitions are adapted from Currah 1985, Kirk *et al.* 2001, Currah 2004, Rice & Currah, in press.

Acidophilic/Acidophilous: growing at low pH; optimal growth below pH 7 (3-5).

Acropetal conidiogenesis: pattern of conidial formation with the youngest spore at the tip of the chain and the oldest at the base.

Acrotelm: Aerobic surface layer of the peat column where most decomposition occurs.

Aleurioconidium: a single-celled, terminal asexual spore (conidium), that is released through rhexolytic dehiscence.

Anamorph: morphologically distinct, asexual phase of a fungal life cycle.

Apothecium: cup- or disk- shaped ascoma.

Arbuscular mycorrhiza: association between plants and fungi in which the fungus produces tree-like arbuscules within the root cells

Arthroconidium: asexual spore arising from the fragmentation of existing hyphae.

Ascoma/Ascocarp: fruiting body of an ascomycete in which ascospores are formed.

Ascomycete: a general label referring to fungi that produce meiospores in asci.

Ascospores: meiospores produced by ascomycetes within an ascus.

Ascus: sac in which ascospores mature.

Basidiocarp/Basidiome: fruiting body of a basidiomycete in which basidiospores (meiospores) are formed.

Basidiomycete: a general label referring to fungi that produce meiospores on a basidium.

Basidium: terminal cell in which karyogamy and meiosis occurs in basidiomycetes.

Basipetal conidiogenesis: pattern of conidial formation with the oldest spore at the tip of the chain and the youngest at the base.

Biolog FF plates: 96-well microplates produced by Biolog Inc. (California) for the automated identification of filamentous fungi.

Biotroph: an organism capable from extracting nutrients from another organism without killing it.

Brown rot: wood decay in which the cellulose fraction is removed from the cell walls leaving the amorphous, brown lignins.

Catotelm: anaerobic, buried layers of the peat column where little decomposition occurs.

Centrum: the contents of an ascocarp.

Chytrid: general label referring to any fungus that produces flagellated cells.

Chlamydospore: a thick-walled, asexual resting spore.

Clamp connection: buckle-shaped knob over the septum of some basidiomycetes, representing a short hypha through which a nucleus migrated during mitosis.

Cleistothecium: an enclosed peridium found in some ascomycetes.

Commensalism: relationship between individuals of two or more species where there is a positive effect on one partner and no effect on the other (+/0).

Conidium: Asexual spore.

Conidiogenous cell: a cell giving rise to conidia.

Conidiophore: a structure bearing conidia and/or conidiogenous cells.

Coprophilous: describes organisms primarily found on dung.

Crozier: hook formed during the formation of an ascus; homologous with a clamp connection.

Deliquescent: dissolving at maturity.

Dematiaceous: darkly pigmented or melanized.

Ectendomycorrhiza: association between conifers or ericaceous plants and fungi in which the fungus forms distinctive hyphal structures inside and outside the root cortical cells.

Ectomycorrhiza: association between woody plants and fungi in which the fungus forms a mantle on the root surface and a Hartig net between the cells, but does not penetrate the root cells.

Endophyte: a fungus living inside the organs of a living plant.

Ericoid mycorrhiza: association between members of the *Ericaceae* and fungi in which the fungus forms coils inside the root cells.

Fascicular bundles: bundle of hyphae associated with ascocarp.

Fertile hyphae: conidiogenous hyphae.

Fruticose thallus: shrubby growth form in a lichen, erect or pendant.

Geniculate conidiogenesis: mode of conidiogenesis observed in *Myxotrichum arcticum* in which short, truncated chains of conidia are produced in whorls perpendicular to the conidiophore axis.

Gymnothecium: ascocarp where the peridium is a loose hyphal network.

Heterokaryon: fungus with at least two genetically distinct nuclei per cell.

Heterothallic: fungus which cannot self cross and requires a genetically distinct partner.

Holomorph: a concept embodying the entire life cycle of a fungus with all its reproductive and vegetative states.

Hyaline: transparent or colourless.

Hypha: tubular cell that extends by tip growth. Fundamental unit of most fungi.

Hyphomycete: mold, group of asexually reproducing fungi where the spores are exposed at maturity.

Inoperculate discomycetes: group of ascomycetes that produce cup- or disk-shaped ascomata, and ascospores that dehisce via an apical pore in the ascus.

Microspermy: production of tiny, underdeveloped, dust-like seeds by some orchids and *Ericaceae*. These seeds are characteristic of plants that rely on mycorrhizal fungi for carbon nutrition and tend to germinate only in the presence of mycorrhizal partners.

Monophyletic: group (clade) consisting of all of the descendents of a single common ancestor.

Mycelium: a mass of hyphae.

Mycobiont: fungal partner in symbiotic relationships, including lichens and mycorrhizas.

Mycorrhiza: close, mutualistic, physical association of plant root and fungus.

Paraphyletic: group (clade) that includes only some descendants of a common ancestor but excludes other descendents of that ancestor

Peat: heterogeneous assemblage of plant and animal remains that accumulates in a peatland due to slow decomposition.

Peatland: wetland that accumulates organic matter as peat due to slow decomposition.

Peloton: fungal structure produced inside the root cells of orchids, digested by the plant to provide nutrients.

Peridium: outer wall of a fruiting body; composed of hyphae (peridial elements) that surround the ascospores and asci of a cleistothecium.

Perispore: sheath or membrane surrounding a spore.

Phenol-oxidizing enzymes: enzymes responsible for the breakdown of polyphenolic compounds; examples include laccases, lignin-peroxidases.

Polyphyletic: group (clade) that includes taxa that do not share a common ancestor.

Pseudoparenchyma: thick tissue formed by hyphae that are twisted and fixed together and no longer resemble discrete hyphae.

Psychrophilic: growing optimally at cool temperatures (typically less than 20°C)

Psychrotolerant: growing at temperatures below 10 °C.

Reticuloperidium: peridium of a gymnothecial ascomycetes, a mesh-like, loose arrangement of peridial hyphae.

Rhexolytic dehiscence: mode of conidial dehiscence whereby the membrane of the intervening cell between two conidia is ruptured.

Rhizosphere: region immediately surrounding a root and influenced by its presence.

Saprobe: uses dead material as a source of carbon and energy.

Schizolytic dehiscence: mode of condial dehiscence where separation occurs at the septum between two conidia.

Soft rot: wood decay produced by ascomycetes in which cellulose, polysaccharides, and sometimes lignin are removed.

Sporodochium: a cushion-shaped body on which asexual spores are produced.

Synnema: a group of erect, often fused conidiophores with conidial production at or near the apex.

Telaperidium: envelope of thin-walled hyphae surrounding the centrum that lack any obvious differentiation from vegetative hyphae.

Teleomorph: morphologically distinct, sexual phase of a fungal life cycle.

White rot: wood decay in which the lignin is removed to leave the pale coloured cellulose residues.

Zygomycete: a general term for any fungus that produces a zygospore (resting cell) prior to meiosis.

Literature Cited

Currah RS (1985). Taxonomy of the *Onygenales*: *Arthrodermataceae, Gymnoascaceae, Myxotrichaceae* and *Onygenaceae*. *Mycotaxon* **24**: 1–216.

Currah RS (2004). *Botany 306: Biology of the Fungi. A Laboratory Manual*. University of Alberta, Edmonton, AB, Canada.

Kirk PM, Cannon PF, David JC, Stalpers JA (2001). *Dictionary of the Fungi, 9th Edition*. CABI Biosciences, UK.

Rice AV, Currah RS (in press 2). *Oidiodendron maius*: Saprobe in *Sphagnum* peat, mutualist in ericaceous roots? In: Schulz B, Boyle C, Sieber T (eds) *Microbial Root Endophytes*. Springer-Verlag, Heidelberg (Accepted Jan. 2005).